UNIVERSIDADE FEDERAL DE SANTA CATARINA
CENTRO DE CIÊNCIAS BIOLÓGICAS
DEPARTAMENTO DE ECOLOGIA E ZOOLOGIA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

RICARDO FILIPE RIFFEL

INFLUÊNCIA DE FATORES FÍSICOS NA COMPOSIÇÃO DA COMUNIDADE BÊNTICA DE SUBSTRATO CONSOLIDADO EM DIFERENTES ESCALAS NO LITORAL DE SANTA CATARINA

Florianópolis
2016

Ricardo Filipe Riffel

INFLUÊNCIA DE FATORES FÍSICOS NA COMPOSIÇÃO DA COMUNIDADE BÊNTICA DE SUBSTRATO CONSOLIDADO EM DIFERENTES ESCALAS NO LITORAL DE SANTA CATARINA

Dissertação submetida ao Programa de Pós-Graduação em Ecologia da Universidade Federal de Santa Catarina para a obtenção do Grau de Mestre em Ecologia

Orientador: Prof. Dr. Alberto Lindner

Florianópolis
2016

Ficha de identificação da obra elaborada pelo autor,
através do Programa de Geração Automática da Biblioteca Universitária da UFSC.

Riffel, Ricardo Filipe
INFLUÊNCIA DE FATORES FÍSICOS NA COMPOSIÇÃO DA COMUNIDADE BÊNTICA DE SUBSTRATO CONSOLIDADO EM DIFERENTES ESCALAS NO LITORAL DE SANTA CATARINA / Ricardo Filipe Riffel ; orientadora, Alberto Lindner - Florianópolis, SC, 2016.
71 p.

Dissertação (mestrado) - Universidade Federal de Santa Catarina, Centro de Ciências Biológicas. Programa de Pós Graduação em Ecologia.

Inclui referências

1. Ecologia. 2. Distribuição da comunidade bêntica de costões rochosos. 3. Processos multi escala. 4. Padrões latitudinais. 5. Substituição de espécies. I. Lindner, Alberto. II. Universidade Federal de Santa Catarina. Programa de Pós-Graduação em Ecologia. III. Título.

"**Influência de fatores físicos na composição da comunidade bêntica de substrato consolidado em diferentes escalas no litoral de Santa Catarina**"

Por

Ricardo Filipe Riffel

Dissertação julgada e aprovada em sua forma final pelos membros titulares da Banca Examinadora (04/PPGECO/2016) do Programa de Pós-Graduação em Ecologia - UFSC.

Prof(a). Dr(a). Nivaldo Peroni
Coordenador(a) do Programa de Pós-Graduação em Ecologia

Banca examinadora:

Dr(a) Alberto Lindner (Universidade Federal de Santa Catarina)
Orientador(a)

Dr(a) Augusto Alberto Valero Flores (Universidade de São Paulo - videoconferência)

Dr(a) José Bonomi Barufi (Universidade Federal de Santa Catarina)

Dr(a) Carlos Frederico Gurgel (Universidade Federal de Santa Catarina)

Florianópolis, 10 de março de 2016.

Aos drivers da minha felicidade: minha família, minha namorada e minha afilhada

AGRADECIMENTOS

Ao Prof. Dr. Alberto Lindner, meu orientador, pelo carinho, amizade, compreensão, valorosas observações e pela oportunidade do desenvolvimento deste trabalho em seu laboratório. Foram de grande valia todos os conhecimentos transmitidos.

Ao prof. Dr. Leonardo Sandrini Neto, por sua ajuda essencial na avaliação estatística dos meus dados e seus pacientes ensinamentos nesta difícil disciplina.

A toda equipe do Laboratório de Biodiversidade Marinha pelo auxílio nas mais diversas etapas no desenvolvimento deste trabalho e de tantos outros, sempre muito solícitos e gentis. Meus sinceros agradecimentos por todas as ajudas, risadas e por ouvirem sempre minhas angústias. Admiro muito o trabalho de todos vocês.

A todos os colaboradores em campo, principalmente João Pedro Barros, Jonathan Wanderley Lawley, Helora Torres e Flora Sarti que contribuiram muito nos árduos trabalhos de campo em praias maravilhosas.

Aos profissionais que me auxiliaram com a identificação das espécies: João de Fraga Carraro (Esponjas), Laura Pioli Kramer (ascídias), Vanessa Freire e Manuela Batista (algas) e Edson Faria Júnior (cnidários), muito obrigado pelo esforço de todos em me auxiliar a buscar o melhor resultado em meu trabalho.

As intituições de financiamento a pesquisa no Brasil, Capes pelo suporte concedido durante todo o mestrado, CNPQ e ao projeto Biodiverisidade Marinha/FAPESC.

Ao PPG-Ecologia e todos os professores atuantes do programa, por seu empenho em formar ecólogos de excelência.

A todos os professores e funcionários da Universidade Federal de Santa Catarina que ao longo dos últimos 7 anos colaboraram significativamente para a minha formação profissional e pessoal, meus sinceros agradecimentos e admiração.

Em especial...

Aos meus pais, Roque Riffel e Dearlete Marta Riffel, por sempre me apoiarem em minhas escolhas, mesmo quando não concordavam com elas e sabiam que não era a melhor dentre as possíveis. Pelo amor incondicional, por terem feito o possível para nunca me deixar nada faltando, por me deixarem como maior herança a minha educação, meus valores e princípios. Por terem me passado as direções certas a seguir ao longo de minha vida através de exemplos e por terem me demonstrado, através do amor que um sente pelo outro, que este é o maior bem de todos e com certeza não tem fim. A vocês, meus exemplos de perseverança, integridade e sucesso, meu eterno agradecimento, amor e orgulho.

A minha namorada, Mayara Anselmi, não há palavras para descrever todo meu amor por ti e gratidão por tudo o que compartilhamos ao longo destes mais de 6 anos. Muito de toda a minha felicidade e alegria de viver vêm de ti. Obrigado por estar comigo ao longo de toda a graduação e mestrado e compartilhar não somente as horas de estudo, mas também os sonhos e os momentos marcantes. Obrigado por ser tão perfeita e por ter entrado em minha vida.

As minhas irmãs, Rafaela e Carla, pelo amor e companhia em todos os momentos desde a infância que me fizeram refletir e melhorar como pessoa. Me orgulho muito de vocês e espero conseguir ser tão especial como vocês são.

A minha oma e meu opa, e minha avó, por me ajudarem a crescer, contarem suas estórias magníficas e me fazerem dar boas risadas, tenho certeza que vocês estarão sempre do meu lado, não importa onde.

A família Anselmi, que vejo tão pouco mas tenho apreço tão grande, pela confiança depositada em mim, por todo carinho, simpatia e por serem sogros tão maravilhosos.

Aos todos meus amigos e amigas, que compartilharam comigo as expectativas e angústias durante todo o mestrado.

Por vezes sentimos que aquilo que fazemos não é senão uma gota de água no mar. Mas o mar seria menor se lhe faltasse uma gota".

(Madre Teresa de Calcutá)

RESUMO

As comunidades biológicas costumam se dispor de acordo com diferentes mecanismos que influenciam o estabelecimento das espécies em determinado local. Estes processos ocorrem em diferentes escalas e são responsáveis por variações em diferentes níveis hierárquicos. Neste estudo, buscamos identificar se existe um padrão de distribuição da comunidade bêntica em três escalas diferentes e testamos a influência que três variáveis ambientais atuando em diferentes escalas exercem sobre a comunidade bêntica em uma área de transição de ambientes marinhos subtropicais e temperados. Foram amostrados 10 costões rochosos rasos (até 2 metros de profundidade) ao longo de 208km da costa de Santa Catarina. Em cada um dos locais foram dispostos 6 transectos junto aos costões e fotografados 10 quadrats por transceto. Foram medidas três variáveis que podem influenciar na distribuição da comunidade ao longo dos níveis de replicação: temperatura, complexidade e inclinação do substrato. Ao longo do gradiente latitudinal há uma substituição dos grupos de espécies dominantes, sendo zoantídeos e macroalgas coriáceas mais abundantes nos sítios ao norte enquanto que macroalgas calcáreas articuladas, corticadas e filamentos são mais abundantes nos sítios de maior latitude. Para toda a comunidade, assim como para a maior parte das assembleias, a maior variação ocorreu na menor escala, quadrats. As três variáveis ambientais explicam 30.7% da variação total encontrada para a comunidade, sendo que temperatura foi a principal delas e aparentemente interfere na distribuição de zoantídeos, grupo dominante nos sítios mais ao norte. Algas coriáceas são mais abundantes em locais pouco complexos, provavelmente devido a estes locais abrigarem menor diversidade de herbívoros. Inclinação possui pouca influência sobre a composição da comunidade, possivelmente devido à profundidade em que o estudo foi conduzido, o que permite que a radiação solar, principal recurso aliado a diferentes inclinações, se dissipe de forma mais equitativa sobre as diferentes inclinações. Entretanto, outros processos podem estar associados as variações encontradas entre os sítios como diferenças nas concentrações de nutrientes e sedimentação.

Palavras-chave: Escala espacial, Design hierárquico, Estrutura hierárquica, Costões rochosos, comunidade bêntica.

ABSTRACT

Biological communities are distributed over different habitats according to different environmental mechanisms that act filtering species that will form the community. These processes take place in different scales and are responsible for species switches, leading to community dissimilarities over different hierarchical levels. In this study, we aimed to evaluate the distribution patterns of benthic communities at three hierarchical scales, ranging from few meters to hundreds of kilometers. We also tested the effect that sea surface temperature (SST), habitat complexity and susbstrate slope, operating in different scales, exert in shallow water benthic communities in a marine transition zone from subtropical to temperate habitats. Ten shallow rocky shores (up to two meters deep) were sampled along the Santa Catarina coast, southern Brazil. In each site, six transects were disposed parallel the rocky shore and 10 photoquadrats were taken per transect. Over the latitudinal gradient arises a distribution pattern of northern sites dominated by zoanthids and leathery macroalgae while in further south sites articulated calcareous, corticated and filamentous macroalgae were more abundants. The highest variation proportion was concentrated in the lower replication scale: quadrats, corresponding for 50.55% of total variance of the community structure. As well, quadrats aggregate the higher variance for most of species assemblages, possibly ocurring due to the patchy distribution and other micro-processes. Environmental variables assembled were able to jointly explain 30.7% of total community variation. Temperature appears to directly interfere in zoanthid distribution, the dominant group in northern sites, what possibly triggers the species replacement over the latitudinal gradient. Leathery macroalgae are more abundant in low complexity transects, which can be explained by the fact that these places houses lower diversity of vertebrates that feed on fleshy algae. Bottom slope has little effect over community composition; this result may be related to the shallow depth we sampled, which allows solar radiation to affect more equally all different inclination levels. Results shows that although these three variables explain much of total benthic

community variation, other processes may be responsible for approximately 70% of the community change.

Keywords: Spatial scale, Hierarchical design, Hierarchical structure, Rocky shores, Benthic community

LISTA DE FIGURAS

algae, EAM = Ephilitic algal matrix, SPO = Sponges, CNI = Cnidarian, ZOA = Zoanthids, BRY = Bryozoans, URC = Sea urchins, TUN = Tunicates, BIV = Bivalve. ● = Barra da Lagoa, ■ = Ingleses, ◆ = Matadeiro, ● = Sepultura, ■ = Estaleiro, ◆ = Penha, ▲ = Taquaras, ▼ = Paz Island, ● = Vigia, ■ = Batuta Island.

LISTA DE TABELAS

MATERIAL SUPLEMENTAR

LISTA DE SÍMBOLOS, ABREVIATURAS E SIGLAS

Sítios amostrados

- ▼ PAZ = Ilha da Paz
- ◆ PEN = Penha
- ▲ TAQ = Taquaras
- ■ EST = Estaleiro
- ● SEP = Sepultura
- ■ ING = Ingleses
- ● BAR = Barra da Lagoa
- ◆ MAT = Matadeiro
- ● VIG = Vigia
- ■ BAT = Ilha do Batuta

Grupos funcionais/taxonômicos

ACM = Macroalga calcárea articulada

BIV = Bivalves

BRY = Briozoários

CFM = Macroalga corticada foliosa

CNI = Cnidários

CRM = Macroalga crostosa

CTM = Macroalga corticada

EAM = Matriz epilítica de algas

FIM = Algas filamentosas

FLM = Macroalga foliosa

LTM = Macroalga coriácea

SPO = Esponjas

TUN = Tunicados

URC = Ouriços

ZOA = Zoantídeos

Demais abreviaturas e siglas

TSM/SST = Temperatura superficial do mar

ACAS/SACW = Águas centrais do Atlântico Sul

SUMÁRIO

INTRODUÇÃO

A forma como processos podem determinar as características estruturais de uma comunidade biológica vêm sendo objeto de estudo há muitos anos (Turner 1989). As primeiras observações relacionando os atributos de uma diferentes comunidades com as respectivas variações abióticas foram feitas no início do século XX por Gleason, que acreditava que os padrões dissimilares entre comunidades ocorriam em resposta a variação de gradientes ambientais (Gleason 1926). Esses estudos embasaram novos conceitos que atribuíam à variáveis ambientais o status metafórico de filtros ambientais, que dentre a diversidade de espécies que ocorreriam em escala regional, atuariam selecionando as espécies aptas a formar a comunidade a partir de traços ou fenótipos aptos a se estabelecer e persistir no local (Belyea and Lancaster 1999).

Entretanto, apenas mais recentemente ecólogos abordaram o tema de forma holística, buscando entender a forma como micro-processos (aqueles que atuam na pequena escala, a nível de indivíduos) interferem na macro-comunidade e vice-versa (e.g., Witman et al. 2004, 2015, Fraschetti et al. 2005, Eidens et al. 2015). Assim, entender como a estrutura das comunidades varia ao longo de diferentes escalas espacias é crucial para entender quais processos estão associados às dissimilaridades entre locais e comunidades. Este conhecimento também é essencial para procedimentos de conservação e manejo (Underwood et al. 2000).

Para a comunidade bêntica, uma ampla diversidade de processos atuam estruturando sua composição e podem ser responsáveis diretos por diferenças entre comunidades biológicas em diferentes escalas. Dentre esses processos, alguns são intrínsecos de variações ambientais, como a ação das ondas, capaz de selecionar diferentes organismos de acordo com diferentes condições de hidrodinamismo (Madin and Connolly 2006, Flores et al. 2015); radiação solar, que é recurso essencial ao estabelecimento de organismos fotossintetizantes (Jokiel 1980, Llabrés et al. 2013); concentração de nutrientes, que pode causar variações sazonais na comunidade com a ocorrência de eventos como ressurgência (Smith et al. 2001); e profundidade, que carrega consigo um gradiente de variações em diversas outras variáveis ambientais, sobretudo temperatura e luminosidade (Garrabou et al. 2002, Williams et al. 2013).

Alguns outros processos podem ser fortemente modificados por ações humanas, como turbidez (Airoldi 2003), sedimentação (Connell 2005), sobrecarga de nutrientes (McCook 1999), desenvolvimento costeiro (que pode levar ao aumento de descargas de poluição nos oceanos; Fabricius 2005, Puente and Diaz 2015) e a introdução acidental de espécies invasoras (e.g., Creed 2006, Lages et al. 2011); as quais podem desencadear uma série de distúrbios ecológicos em ambientes marinhos (Grigg 1995, Jackson 2001).

Temperatura apresenta forte influência em escala regional na composição da comunidade bêntica marinha, uma vez que diversas espécies de invertebrados marinhos e algas possuem restrições termais de ocorrência tornando-se uma barreira a dispersão de espécies caracterizadas por suportar uma pequena amplitude térmica (Fitt et al. 2001, Reimer et al. 2008, Tronholm et al. 2012). Por exemplo, um estudo recente indica que a distribuição de antozoários zooxantelados é influenciada pela frequência de ocorrência de temperaturas abaixo de 16°C em Santa Catarina (Faria-Júnior 2014). Para zoantídeos, existe uma distribuição descontínua entre costões rochosos do sudeste e sul brasileiros, ocorrendo uma queda gradual nas abundâncias relativas até a ausência, ao longo do gradiente latitudinal, sendo essa variação associada à diminuição da temperatura superficial do mar (TSM) média (Oliveira 2014). Desta forma, com a temperatura influenciando a distribuição de determinados táxons, ocorre uma substituição de espécies ao longo do gradiente decrescente de TSM (Fernandez et al. 2015).

A complexidade do hábitat também pode ser um importante preditor da comunidade no nível local, já que locais excepcionalmente complexos abrigam uma maior diversidade de espécies (Aguilera et al. 2014, Bloch and Klingbeil 2015) e de interações (Johnson et al. 1998) em comparação com locais menos complexos. Da mesma forma, em micro-escala, a inclinação do substrato também pode ser responsável por variações da comunidade, criando um gradiente de abundância ao longo das diferentes classes de inclinação devido a preferências de assentamento larval (Mizrahi et al. 2014).

Ao longo do Atlântico Sul, o estado de Santa Catarina (Brasil) é uma região de transição entre os ambientes marinhos subtropical e temperado (Floeter et al. 2008), possuindo grande

importância biogeográfica para organismos bênticos, sendo o limite sul de distribuição de zoantídeos zooxantelados (Bouzon et al., 2012), corais recifais (Castro and Pires 2001, Capel et al. 2012), peixes recifais e outros invertebrados (e.g., Floeter et al. 2008, Anderson et al. 2015). A costa de Santa Catarina também recebe influências de diversas massas de água, como a corrente do Brasil, de águas mais quentes, vinda do norte, e as águas centrais do Atlântico Sul (ACAS), mais frias e ricas em nutrientes. Existem ainda massas sazonais que influenciam a plataforma continental e podem interferir na dinâmica das comunidades de costões rochosos, como águas subantárticas que atingem a costa durante os meses de inverno, assim como a pluma do Rio da Prata, que durante o inverno se extende mais ao norte, chegando a ilha de Santa Catarina (Acha et al., 2004; Piola et al., 2000). Devido a atuação de massas de água com características distintas, a temperatura superficial varia de 14°C no Inverno a 28°C no verão (Faria-Júnior 2014). Essa amplitude térmica implica em diversas alterações na composição e abundâncias das espécies bênticas (Menge et al. 1997).

Para entender a forma como processos atuam estruturando a comunidade ao longo de diferentes escalas é necessário que o desenho amostral compreenda diferentes escalas de replicagem da comunidade, sendo a forma mais apropriada para avaliar suas dissimilaridades (Morrisey et al. 1992, Underwood and Chapman 1996, Underwood 1997). Um padrão recorrente encontrado em costões rochosos é a maior variação estar concentrada no menor nível hirárquico amostrado (Fraschetti et al. 2001, Chapman 2002, Coleman 2002). Provavelmente, esta alta dissimilaridade concentrada no menor nível hierárquico é regulada por processos que atuam em menor escala, como interações que ocorrem localmente entre organismos, comportamento das espécies, e processos físicos em pequena escala como a sedimentação e inclinação do substrato (Benedetti-Cecchi 2001).

A maioria das pesquisas marinhas em diferentes níveis hierárquicos visando encontrar padrões espaciais de populações e comunidades permanecem limitadas a poucos hábitats, são conduzidas em pequena escala (dezenas de km), e restritas a assembleias específicas, sendo um padrão recorrente nos costões rochosos a variância estar concentrada no menor nível hierárquico. Além do mais, poucos estudos foram feitos na

América do Sul (Fraschetti et al. 2005), o que demonstra a falta de estudos de larga escala que busquem padrões para toda a comunidade bêntica nessa região.

Um importante padrão latitudinal na comunidade bêntica é a gradual substituição de cnidários, dominantes em recifes tropicais, por macroalgas, que possuem seu ápice de biodiversidade e biomassa em regiões temperadas (Kerswell 2006). Um dos fatores que possivelmente explicam esse gradual padrão de substituição com o aumento de riqueza e abundância em direção aos polos é a competição com corais, que possivelmente podem regular sua distribuição e abundâncias (Miller and Hay 1996, McCook et al. 2001). Assim como a intensa herbivoria nos trópicos, que pode regular sua abundância e evolução (Bellwood 2003, Floeter et al. 2005).

Este estudo visa: i) identificar se a estrutura da comunidade bêntica rasa varia ao longo da costa de Santa Catarina, em um gradiente latitudinal; ii) investigar a estrutura da comunidade bêntica rasa a partir de diferentes escalas de amostragem (centímetros a dezenas de quilômetros) e iii) compreender se Temperatura Superficial do Mar (TSM), complexidade de hábitat e inclinação do substrato influenciam na composição e distribuição da comunidade bêntica. Nossas hipóteses de trabalho são i) ocorrerá um padrão de substituição de espécies de cnidários por algas frondosas ao longo do gradiente latitudinal; ii) a maior variação na comunidade bêntica séssil estará concentrada no menor nível hierárquico (quadrats) e iii) as três variáveis ambientais acima citadas irão exercer forte influência na comunidade, agindo de forma específica em cada assembleia. Por exemplo alguns cnidários possuem um limiar térmico de ocorrência e assim podem ter sua distribuição modificada ao longo do gradiente de temperatura. Da mesma forma, algas, que necessitam de radiação solar, podem ser mais abundantes em costões planos em relação a costões inclinados.

REFERÊNCIAS

Acha, E. M., H. W. Mianzan, R. A. Guerrero, M. Favero, and J. Bava. 2004. Marine fronts at the continental shelves of austral South America. Journal of Marine Systems 44:83–105.

Aguilera, M. A., B. R. Broitman, and M. Thiel. 2014. Spatial variability in community composition on a granite breakwater versus natural rocky shores: lack of microhabitats suppresses intertidal biodiversity. Marine pollution bulletin 87:257–68.

Airoldi, L. 2003. The effects of sedimentation on rocky coast assemblages. Oceanography and Marine Biology 41:161–236.

Anderson, A. B., A. Carvalho-filho, R. A. Morais, L. T. Nunes, J. P. Quimbayo, and S. R. Floeter. 2015. Brazilian tropical fishes in their southern limit of distribution: checklist of Santa Catarina's rocky reef ichthyofauna, remarks and new records 11.

Bellwood, D. R. 2003. Origins and escalation of herbivory in fishes: a functional perspective. Paleobiology 29:71–83.

Belyea, L. R., and J. Lancaster. 1999. Assembly Rules within a Contingent Ecology. Oikos 86:402–416.

Benedetti-Cecchi, L. 2001. Variability in abundance of algae and invertebrates at different spatial scales on rocky sea shores. Marine Ecology Progress Series 215:79–92.

Bloch, C. P., and B. T. Klingbeil. 2015. Anthropogenic factors and habitat complexity influence biodiversity but wave exposure drives species turnover of a subtropical rocky inter-tidal metacommunity. Marine Ecology 1:1–13.

Bouzon, J., F. P. Brandini, and R. M. Rocha. 2012. Biodiversity of Sessile Fauna on Rocky Shores of Coastal Islands in Santa Catarina, Southern Brazil. Marine Science 2:39–47.

Capel, K. C. C., B. Segal, P. Bertuol, and A. Lindner. 2012. Corallith beds at the edge of the tropical South Atlantic. Coral Reefs.

Castro, C. B., and D. O. Pires. 2001. Brazilian Coral Reefs: What we alredy know and what is still missing. Bulletin of Marine Science 69:357–371.

Chapman, M. G. 2002. Patterns of spatial and temporal variation of macrofauna under boulders in a sheltered boulder field. Austral Ecology 27:211–228.

Coleman, M. . 2002. Small-scale spatial variability in intertidal and subtidal turfing algal assemblages and the temporal generality of these patterns. Journal of Experimental Marine Biology and Ecology 267:53–74.

Connell, S. D. 2005. Assembly and maintenance of subtidal habitat heterogeneity : synergistic effects of light penetration and sedimentation. Marine Ecology Progress Series 289:53–61.

Creed, J. C. 2006. Two invasive alien azooxanthellate corals, Tubastraea coccinea and Tubastraea tagusensis, dominate the native zooxanthellate Mussismilia hispida in Brazil. Coral Reefs.

Eidens, C., T. Hauffe, E. Bayraktarov, C. Wild, and T. Wilke. 2015. Multi-scale processes drive benthic community structure in upwelling-affected coral reefs. Frontiers in Marine Science 2:1–11.

Fabricius, K. E. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Marine pollution bulletin 50:125–46.

Faria-Júnior, E. 2014. Distribuição espacial e estrutura das comunidades de antozoários (cnidaria: anthozoa) em substratos consolidados no litoral de santa catarina, sul do Brasil. Dissertação (mestrado) Programa de Pós-Graduação em Ecologia - Universidade Federal de Santa Catarina.

Fernandez, M. O., S. A. Navarrete, and A. C. Marques. 2015. A comparison of temporal turnover of species from benthic cnidarian assemblages in tropical and subtropical harbours. Marine Biology Research 11:492–503.

Fitt, W., B. Brown, M. Warner, and R. Dunne. 2001. Coral bleaching: interpretation of thermal tolerance limits and thermal thresholds in tropical corals. Coral Reefs 20:51–65.

Floeter, S. R., M. D. Behrens, C. E. L. Ferreira, M. J. Paddack, and M. H. Horn. 2005. Geographical gradients of marine herbivorous fishes: Patterns and processes. Marine Biology 147:1435–1447.

Floeter, S. R., L. A. Rocha, D. R. Robertson, J. C. Joyeux, W. F. Smith-Vaniz, P. Wirtz, A. J. Edwards, J. P. Barreiros, C. E. L. Ferreira, J. L. Gasparini, A. Brito, J. M. Falcón, B. W.

Bowen, and G. Bernardi. 2008. Atlantic reef fish biogeography and evolution. Journal of Biogeography 35:22–47.

Flores, A. A. V., R. A. Christofoletti, A. L. F. Peres, A. M. Ciotti, and S. A. Navarrete. 2015. Interactive effects of grazing and environmental stress on macroalgal biomass in subtropical rocky shores: Modulation of bottom-up inputs by wave action. Journal of Experimental Marine Biology and Ecology 463:39–48.

Fraschetti, S., C. N. Bianchi, A. Terlizzi, G. Fanelli, C. Morri, and F. Boero. 2001. Spatial variability and human disturbance in shallow subtidal hard bottom assemblages: a regional approach. Marine Ecology Progress Series 212:1–12.

Fraschetti, S., A. Terlizzi, and L. Benedetti-cecchi. 2005. Patterns of distribution of marine assemblages from rocky shores : Evidence of relevant scales of variation. Marine Ecology Progress Series 296:13–29.

Garrabou, J., E. Ballesteros, and M. Zabala. 2002. Structure and Dynamics of North-western Mediterranean Rocky Benthic Communities along a Depth Gradient. Estuarine, Coastal and Shelf Science 55:493–508.

Gleason, H. A. 1926. The Individualistic Concept of the Plant Association. Bulletin of the Torrey Botanical Club 53:7–26.

Grigg, R. W. 1995. Coral reefs in an urban embayment in Hawaii: a complex case history controlled by natural and anthropogenic stress. Coral Reefs 14:253–266.

Jackson, J. B. 2001. What was natural in the coastal oceans? Proceedings of the National Academy of Sciences of the United States of America 98:5411–5418.

Johnson, M. P., R. N. Hughes, M. T. Burrows, and S. J. Hawkins. 1998. Beyond the predation halo: small scale gradients in barnacle populations affected by the relative refuge value of crevices. Journal of Experimental Marine Biology and Ecology 231:163–170.

Jokiel, P. L. 1980. Solar ultraviolet radiation and coral reef epifauna. Science 207:1069–1071.

Kerswell, A. P. 2006. Global biodiversity patterns of benthic marine algae. Ecology 87:2479–2488.

Lages, B. G., B. G. Fleury, C. Menegola, and J. C. Creed. 2011. Change in tropical rocky shore communities due to an alien

coral invasion. Marine Ecology Progress Series 438:85–96.
Llabrés, M., S. Agustí, M. Fernández, A. Canepa, F. Maurin, F. Vidal, and C. M. Duarte. 2013. Impact of elevated UVB radiation on marine biota: a meta-analysis. Global Ecology and Biogeography 22:131–144.
Madin, J. S., and S. R. Connolly. 2006. Ecological consequences of major hydrodynamic disturbances on coral reefs. Nature 444:477–480.
McCook, L. J. 1999. Macroalgae, nutrients and phase shifts on coral reefs: Scientific issues and management consequences for the Great Barrier Reef. Coral Reefs 18:357–367.
McCook, L. J., J. Jompa, and G. Diaz-Pulido. 2001. Competition between corals and algae on coral reefs: A review of evidence and mechanisms. Coral Reefs 19:400–417.
Menge, B. A., B. A. Daley, P. A. Wheeler, E. Dahlhoff, E. Sanford, and P. T. Strub. 1997. Benthic-pelagic links and rocky intertidal communities: Bottom-up effects on top-down control? Proceedings of the National Academy of Sciences 94:14530–14535.
Miller, M. W., and M. E. Hay. 1996. Coral-Seaweed-Grazer-Nutrient Temperate Reefs1. Ecological Monographs 66:323–344.
Mizrahi, D., S. A. Navarrete, and A. A. V. Flores. 2014. Uneven abundance of the invasive sun coral over habitat patches of different orientation: An outcome of larval or later benthic processes? Journal of Experimental Marine Biology and Ecology 452:22–30.
Morrisey, D. J., A. J. Underwood, L. Howitt, and J. S. Stark. 1992. Temporal variation in soft-sediment benthos. Journal of Experimental Marine Biology and Ecology 164:233–245.
Oliveira, A. F. S. de. 2014. Aspectos biológicos e ecológicos de zoantídeos zooxantelados em costões rochosos do sul e sudeste do Brasil. Dissertação (mestrado) Programa de Pós-Graduação em Ecologia - Universidade Federal de Santa Catarina.
Piola, A. R., E. J. D. Campos, O. O. Moller Jr., M. Charo, C. Martinez, E. J. D. Campos, O. O. Moller Jr, M. Charo, and C. Martinez. 2000. Subtropical Shelf Front off eastern South America. Journal of Geophysical Research 105:6565–6578.
Puente, A., and R. J. Diaz. 2015. Response of benthos to ocean

outfall discharges: does a general pattern exist? Marine pollution bulletin 101:174–181.

Reimer, J. D., S. Ono, F. Sinniger, and J. Tsukahara. 2008. Distribution of zooxanthellate zoanthid species (Zoantharia: ANthozoa: Hexacorallia) in southern Japan limited by cold temperatures. Galaxea, Journal of Coral Reef Studies 10:57–67.

Smith, J. E., C. M. Smith, and C. L. Hunter. 2001. An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. Coral Reefs 19:332–342.

Tronholm, A., F. Leliaert, M. Sansón, J. Afonso-Carrillo, L. Tyberghein, H. Verbruggen, and O. de Clerck. 2012. Contrasting geographical distributions as a result of thermal tolerance and long-distance dispersal in two allegedly widespread tropical brown algae. PLoS ONE 7.

Turner, M. G. 1989. Landscape Ecology: The Effect of Pattern on Process. Annual Review of Ecology and Systematics 20:171–197.

Underwood, A. ., M. . Chapman, and S. . Connell. 2000. Observations in ecology: you can't make progress on processes without understanding the patterns. Journal of Experimental Marine Biology and Ecology 250:97–115.

Underwood, A., and M. Chapman. 1996. Scales of spatial patterns of distribution of intertidal invertebrates. Oecologia 107:212–224.

Underwood, A. J. 1997. Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance. Cambridge University Press, Cambridge.

Williams, G. J., J. E. Smith, E. J. Conklin, J. M. Gove, E. Sala, and S. A. Sandin. 2013. Benthic communities at two remote Pacific coral reefs: effects of reef habitat, depth, and wave energy gradients on spatial patterns. PeerJ 1:e81.

Witman, J. D., R. J. Etter, and F. Smith. 2004. The relationship between regional and local species diversity in marine benthic communities : A global perspective. Proceedings of the National Academy of Sciences of the United States of America 101:15664–9.

Witman, J. D., R. W. Lamb, and J. E. K. Byrnes. 2015. Towards an integration of scale and complexity in marine Ecology. Ecological Monographs 85:475–504.

Capítulo único
(Formatado Segundo os padrões do periódico Journal of Experimental Marine Biology and Ecology)

Multi-scale processes driving marine benthic community structure in a South Atlantic transition zone

Abstract

Biological communities are distributed over different habitats according to different environmental mechanisms that act filtering species that will form the community. These processes take place in different scales and are responsible for species switches, leading to community dissimilarities over different hierarchical levels. In this study, we aimed to evaluate the distribution patterns of benthic communities at three hierarchical scales, ranging from few meters to hundreds of kilometers. We also tested the effect that sea surface temperature (SST), habitat complexity and susbstrate slope, operating in different scales, exert in shallow water benthic communities in a marine transition zone from subtropical to temperate habitats. Ten shallow rocky shores (up to two meters deep) were sampled along the Santa Catarina coast, southern Brazil. In each site, six transects were disposed parallel the rocky shore and 10 photoquadrats were taken per transect. Over the latitudinal gradient arises a distribution pattern of northern sites dominated by zoanthids and leathery macroalgae while in further south sites articulated calcareous, corticated and filamentous macroalgae were more abundants. The highest variation proportion was concentrated in the lower replication scale: quadrats, corresponding for 50.55% of total variance of the community structure. As well, quadrats aggregate the higher variance for most of species assemblages, possibly ocurring due to the patchy distribution and other micro-processes. Environmental variables assembled were able to jointly explain 30.7% of total community variation. Temperature appears to directly interfere in zoanthid distribution, the dominant group in northern sites, what possibly triggers the species replacement over the latitudinal gradient. Leathery macroalgae are more abundant in low complexity transects, which can be

explained by the fact that these places houses lower diversity of vertebrates that feed on fleshy algae. Bottom slope has little effect over community composition; this result may be related to the shallow depth we sampled, which allows solar radiation to affect more equally all different inclination levels. Results shows that although these three variables explain much of total benthic community variation, other processes may be responsible for approximately 70% of the community change.

Highlights:

- Variation over benthic sessile community was higher at the smallest scale
- Temperature exerts strong influence in zoanthids structure
- Habitat complexity may influence leathery macroalgae abundances
- Bottom slope has no direct relationship with community dissimi larities
- There is species replacement along the latitudinal gradient

Keywords: Spatial scale, Hierarchical design, Hierarchical structure, Rocky shores, Benthic community

1. Introduction

The way processes determine community biotic components has been investigated for many years (Turner 1989) . However, only recently ecologists have given a more holistic approach to this issue, trying to understand how micro-processes interfere in macro-community patterns and vice versa (e.g., Witman et al. 2004, 2015, Fraschetti et al. 2005, Eidens et al. 2015). Thus, understanding how community composition and structure vary across different spatial-scales is critical to understand what processes are associated with dissimilarities among sites. This information is also critical for conservation and management procedures (Underwood et al. 2000).

For benthic species, a wide range of processes act structuring community components, some of which depend

exclusively on environmental particularities, such as wave action (Madin and Connolly 2006, Flores et al. 2015), solar radiation (Jokiel 1980, Llabrés et al. 2013), nutrient concentration (Smith et al. 2001) and depth (Garrabou et al. 2002, Williams et al. 2013). On the other hand, some abiotic variables may be strongly influenced by human activities, for example sedimentation (Connell 2005), turbidity (Airoldi 2003), nutrient overload (McCook 1999), coastal development combined with pollution discharges in oceans (Fabricius 2005, Puente and Diaz 2015) and the introduction of alien species (Creed 2006, Lages et al. 2011), which can trigger several ecological changes in marine environments (Grigg 1995, Jackson 2001).

Temperature has a great influence on marine benthic composition at regional scales, since many invertebrates have thermal constraints (e.g., Fitt et al. 2001, Reimer et al. 2008), with species turnover occurring according to sea surface temperature (SST) changes along latitudinal gradients (Fernandez et al. 2015). Habitat complexity may also be an important predictor of community at site level, because exceptionally complex sites house a wider diversity of species (Aguilera et al. 2014, Bloch and Klingbeil 2015) and interactions (Johnson et al. 1998) among benthic organisms, in contrast to low complexity habitats. Similarly, on a micro-scale, the slope of the substrate may be responsible for a population's abundance gradient, due to larval settlement preferences (Mizrahi et al. 2014). This may also lead to variations in benthic community structure, since different levels of inclination receive different intensities of solar radiation, nutrients overload and sedimentation (Prather et al. 2016).

One important latitudinal pattern in benthic community structure is the gradual replacement of cnidarians, dominant in tropical reefs, for algae, which mostly have their biodiversity peak at temperate regions (Kerswell 2006). This gradual shift pattern with an increase of richness and abundances of algae out of the tropics is possibly explained by the intense competition with corals on tropics, which may regulate their abundances and distribution (Miller and Hay 1996, McCook et al. 2001) as well the intense fish grazing on tropics, wich regulate their abundances and evolution (Bellwood 2003, Floeter et al. 2005).

For the southwestern Atlantic, the state of Santa Catarina is an environmental transition zone from subtropical to temperate marine environments (Floeter et al. 2008), thus an important biogeographic zone for benthic organisms (e.g., the southern limit of distribution of zooxanthellate zoanthids, reef corals and reef fishes (Castro and Pires 2001, Floeter et al. 2008, Capel et al. 2012, Bouzon et al. 2012, Anderson et al. 2015). This geographical transition due to several environmental changes implies many shifts in species composition and its abundances (Menge et al. 1997).

Marine hierarchical design studies aimed to investigate spatial patterns of populations and communities over different replicate scales, thus a great tool to understand the influence of abiotic variables over different community scales (Underwood 1997). A recurring pattern for rocky shores assemblages is the highest variance be concentrated on the lower sampled scale (Fraschetti et al. 2001, Chapman 2002, Coleman 2002) probably regulated by small-scale process as local interactions, species behaviour and small-scale physical processes (Benedetti-Cecchi 2001). However, these studies usually are limited to few habitats, small-scales (10s km), and restricted to specific assemblages. Moreover, few studies were carried in South America (Fraschetti et al. 2005), what demonstrates the lack of large-scale studies covering the entire benthic community in this region.

This study aims to: i) identify if the shallow benthic community structure varies along a latitudinal gradient off Santa Catarina; ii) investigate the structure of shallow benthic communities over different sampling scales (centimeters to hundreds of kilometers) and iii) how SST, habitat complexity and bottom slope modify the composition and distribution of benthic community. We hypothesize that i) there is a shift pattern of cnidarians by fleshy algae as most abundant groups over the latitudinal gradient; ii) the largest variation among benthic sessile community will be concentrated in the lower hierarchical level (quadrats) and iii) the three variables will exert strong influence on benthic assemblages distribution, but they will act differently on each group species. For example, species of Cnidaria that have a temperature threshold may have their distributions determined according to the temperature gradient over regional scales.

Similarly, photosynthetic organisms, which require sunlight, may be more abundant in flat than in inclined rocky shores, taking advantage of the higher light incidence in flat surfaces.

2. Methods

2.1 Study site

This research was conduced at 10 rocky shores along 208 km (linear distance) located in Santa Catarina state, southern Brazil, covering the latitudinal coordinates 26°14′36” in the northern site and 28°14′24” in the southernmost site (Figure 1). Santa Catarina coast is known for being a transitional zone between subtropical and temperate marine zones (Floeter et al. 2008), as well the southern boundary of tropical rocky shores for the southwestern Atlantic. Its coastline is influenced by warm water masses from the North through the summer, arising from the Brazilian Current, and the cold and nutrient rich South Atlantic Central Water (SACW). Moreover, during the Winter, the Plata River plume extends northward penetrating more the shelf than in Summer, as well cold water comes from the Subantartic shelf region (Piola et al. 2000, Acha et al. 2004). Due to influences of these different water masses, SST in Santa Catarina ranges from 14°C in Winter to 28°C in Summer (Faria-Júnior 2014).

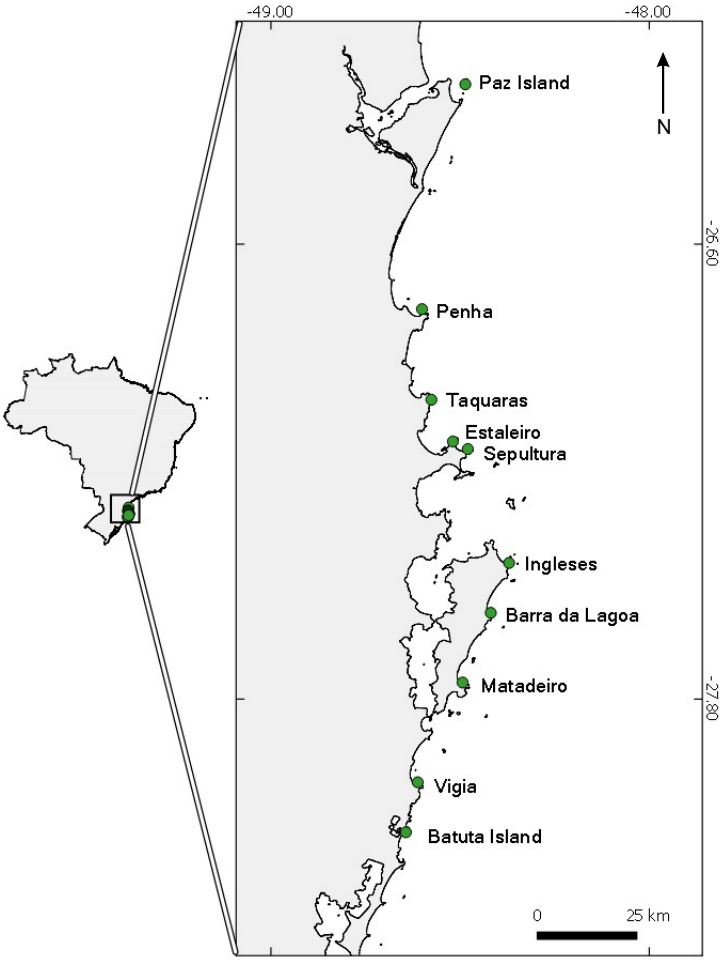


Figure 1 – Study area located in Santa Catarina, southern Brazil. Sampling sites are highlighted in green.

2.2 Sampling procedures

The shallow hard bottom community was sampled from January to April 2015 (Supp.Table 4). In each site, six 20m transects were disposed haphazardly and paralell to the rocky

shore in depths between 1,0 and 2,5 meters. Sampling was performed at low tide periods to ensure sampling only subtidal organisms. A gap of at least 5 meters was left between each transect to avoid pseudo-replicates (WCS-Fiji 2010). Alongside transects, the hard bottom substrate was photographed using 30 cm x 30 cm photoquadrats. Ten photographs were taken in each transect, alternating between right and left sides of the transect, with an interval of two meters for each picture, totaling 60 photoquadrats per site. Benthic community fauna and flora were collected at each site for later identification in laboratory. All 600 images were taken by the same researcher (R. F. Riffel).

2.3 Environmental data

For each site we obtained the sea superficial temperature (SST) data compiled from the GIOVANNI gateway (GES DISC Interactive Online Visualization and Analysis Infrastructure), developed and maintained by NASA Goddard Earth Sciences (GES) Data and Information Services Center (DISC). The spatial resolution was 4 km^2, and the data was gathered for the summer of the last ten years (December to March) according to satellite Aqua, sensor MODIS (Moderate Resolution Imaging Spectroradiometer). The data was extracted to QGIS 2.8.2-Wienand and manipulated to obtain the mean SST for each site for the period selected.

Habitat complexity was visually estimated for each transect according to a complexity scale, ranging from 0 for non-fragmented rocky shores, rectilinear substrates, low rugosity and low slope variation, to 5 for high complex habitat with high variability among rock sizes forming burrows and cracks (Polunin and Roberts 1993, Wilson et al. 2007). The visual estimate of habitat complexity is a reliable, less-effort, low-cost and faster method for assessing rocky shores, providing similar results as more laborious methods as line intercept transects (Wilson et al. 2007).

In order to determine the slope of the rocky shore, a protractor angle was tied to a float and linked to the photoquadrat frame (Faria-Júnior 2014). The measure ranges from 0° to 90° and was determined for each of the 600 photoquadrats.

All locations had the same ripple characteristics, and sampling took place always in places sheltered of the direct effect of waves. All sampled sites were far from any freshwater discharge that could interferer in salinity for each site.

2.4 Data processing

The benthic coverage was analyzed with photoQuad1.0 (Trygonis and Sini 2012). The technique used to estimate the coverage for each species was random points, that randomly superimpose 50 points within a freehanded quadrat over the photoquadrat frame of the original picture. Each point is assigned to species pre-established in a library. The software determines how abundant is the species inside the quadrat and estimates coverage for each species inside the quadrat. This method has similar accuracy of other more laborious techniques, like contouring the real area or using 100 points instead 50 (Drummond and Connell 2005).

Since our main goal was to determine influences of the environment in the benthic sessile community, we determined morphological/taxonomic groups that comprise all of the sampled species. The algal community was classified primarily based in the type of cell organization, thallus strength, and niche, according to Steneck and Dethier (1994) in: filamentous macroalgae (FIM), foliose macroalgae (FLM), corticated foliose macroalgae (CFM), articulated calcareous macroalgae (ACM), crustose macroalgae (CRM), corticated macroalgae (CTM) and leathery macroalgae (LTM), arranged in ascending order of complexity. Ephilitic algal matrix (EAM) is referred here as the micro community formed mainly by a matrix of short turfing algae plus invertebrate cryptofauna, microbes, detritus and sediments (Wilson and Bellwood 1997, Kramer et al. 2012). The fauna was taxonomically classified in bivalves (BIV), bryozoans (BRY), cnidarians, except zoanthids due to high zoanthids representative (CNI), sponges (SPO), tunicates (TUN), sea urchins (URC) and zoanthids (ZOA).

2.5 Statistical analysis

Principal coordinates analysis (PCoA) was used to vizualise differences in overall assemblage structure among sites by a two-dimensional graphical plot where distances among points are ordered closely to their original dissimilarities (sites with similar benthic community structure should be close to each other). PCoA was performed on the basis of the Bray-Curtis dissimilarities on fourth root transformed data (Borcard et al. 2011). Posteriorly, a similarity percentages analysis (SIMPER) was employed to find out which species contributes the most for the dissimilarities among sampling units.

To understand how the variance was distributed among each level of spatial replication for benthic assemblages, we performed a hierarchical design analysis, nested-ANOVA, separately to each functional/taxonomic groups, (Underwood 1997). To determine the contribution of each scale of replication, this analysis acts partitioning total variance amongst different levels of replication or time (in our study, three levels of replication: sites, transects and quadrats). The factors of the model were: sites as fixed effects; transects were the random effect, nested in sites; and quadrats are residual nested inside transects and sites. Therefore, the contribution of each scale of replication for the species assemblages can be determined. Relative abundance to each quadrat data was formerly transformed to arcsine of the square root (Underwood 1997). Cochran`s-test was used to check homogeneity of variances of group species distribution over sites. A *post-hoc* Student-Newman-Keuls (SNK) test was employed to compare differences among sites at $P < 0.05$.

In order to partition the variability of the community structure among the three different treatments we used a permutational multivariate analysis of variance (PERMANOVA) through the PERMANOVA+ add-on package for PRIMER v7 (Anderson et al. 2008), a non-metric test which compartments variability of a data matrix based on any dissimilarity measure in any fully balanced multi factorial ANOVA model, by permutations (Anderson 2001, McArdle and Anderson 2001). Data was formerly transformed to fourth root, and 9999 permutations were executed for a Bray-Curtis distance data matrix. Preceding the analysis, PERMDISP test was employed to

evaluate homogeneity in variances among treatments. There was no uniformity in dispersions, however, for large balanced sampling designs PERMANOVA are unaffected, behaving reliably (see Anderson and Walsh, 2013).

To understand how SST, habitat complexity and bottom slope explain distribution patterns for benthic community, we performed a Constrained Analysis of Principal Coordinates (CAP), a canonical analysis based on principal coordinates (Anderson and Willis 2003). The advantage of this over other constrained analysis is the possibility to use any symmetric distance matrix, which can reduce errors caused by some distance indexes, such as Euclidean and Chi-squared, when analyzing assemblages with several low abundance species or with patchy distribution against highly abundant species (Anderson and Robinson 2003). Species data were formerly transformed to a Bray-Curtis dissimilarity matrix, with fourth root transformation.

Except for PERMANOVA, all statistical analysis and plots were conducted in the software R, version 3.2.2 (R Core Team 2013), combined with GAD (Sandrini-Neto and Camargo 2012), lattice (Sarkar 2008) and vegan (Oksanen et al. 2016) packages.

3. Results

3.1 Hard bottom benthic community structure

Fleshy algae, Epylithic Algal Matrix (EAM) and zoanthids (ZOA) dominated hard-bottom benthic communities in Santa Catarina coast. A total of 68 taxa were identified and classified into 15 functional/taxonomic groups (Supplementary Table 1). Richness varies from 11 species in PAZ, where the community was largely dominated by Zoanthids (ZOA) represententing 72,77% (∓4.35) of total coverage to 32 species in Vigia (VIG) where the community was more evenly distributed, with the most abundant group, EAM, representing 20.70% (∓2.57) of coverage (Figure 3). Each site showed one or more dominant group species (often leaded by a single species), which, in most cases, do not have the same representativeness for other locations (Figure 3).

The SNK test showed a pattern of latitudinal distribution for some taxonomic/functional groups with abundance contrasts or existence restriction along the northern subtropical sites to southern temperate sites. Articulated calcareous macroalgae (ACM), which present a gradual increase of their abundance southwards: the abundance was markedly higher in BAR (30.97% ∓4.23) than in other sites. MAT, VIG and BAT, wich account for 7.57% ∓1.70; 7.43% ∓2.21, and 3.07% ∓1.10 of total coverage, respectively, have their abundances higher than northern sites where the abundance has not reached more than 1.03% ∓0.90 (in EST and absent in PAZ, TAQ and SEP), although the SNK test shows no significant differences among these sites. Corticated macroalgae (CTM) was present in almost all locations, except in PAZ and EST, with minimal abundances of 5.23%, having high importance in structuring benthic community. Despite relatively high abundance in all locations, CTM present an increase in abundances on central and southern sites. ING (29.73% ∓2.96) was higher than BAR and VIG (22.50% ∓3.45 and 22.37% ∓3.02, respectively) which has higher abundances of CTM related to other sites.

Zoanthids (ZOA), present the reverse latitudinal pattern of ACM and CTM, as their abundances were markedly higher in PAZ (72.77% ∓4.35) than in other northern sites (TAQ, SEP with 29.33% ∓4.88 and 36.77% ∓5.33 of total abundances, respectively) and absence in southern sites. Leathery macroalgaes (LTM) are a high distributed group, present in almost every site with high representative, but their abundances are relatively higher in two northern sites EST and PEN, where LTM was the dominat group, representing respectively 55.13% ∓5.13 and 48.06% ∓4.68 of total substrate coverage (Figure 3).

Filamentous macroalgae (FIM) are restricted to southern sites. Although the abundances of Bryozoan (BRY) and Foliose macroalgae (FLM) are relatively small when compared to other species, they also have distribution restrictions according to the latitudinal gradient. Sponges (SPO) gradually enhance their abundances, being more abundant in the cold-water southern sites. Sea urchins (URC), Bivalves (BIV), Tunicates (TUN), Filamentous macroalgae (FIM) and Sponges (SPO) have a markedly higher abundance in only one of the sites. Some group species as Corticated foliose macroalgae (CFM), Cnidarians (CNI), Crustose macroalgae (CRM) and Ephilitic algal matrix (EAM) are more evenly distributed over sites.

The SST data along the Santa Catarina coast show a temperature decline pattern with latitudinal increase. The highest SST mean during the 2015 summer was registered on the northern site (PAZ - 26.31°C), whereas the lowest mean SST was in the southern site (BAT - 23.21°C); having a thermal range of 3.1°C over the study area (Figure 2). However, during the winter months of 2014, the temperature range is slightly lower (1.75°C), once again the highest and lowest mean temperatures were located in the northern and southern extremes (PAZ - 20.1°C and BAT - 18.35°C; Figure 2).

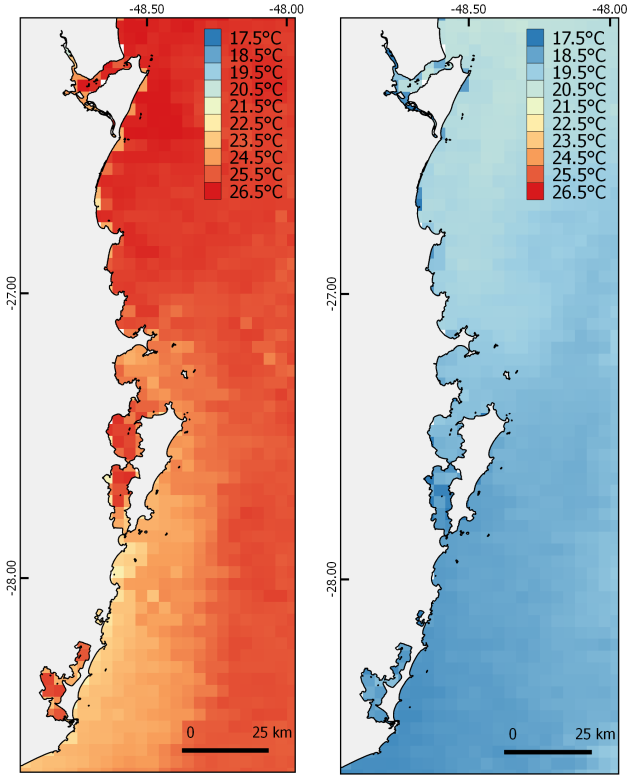


Figure 2 – Mean sea superficial temperature (SST), in Celsius degrees, through Summer (December 2014 – March 2015; Left), and Winter (June 2014 – September 2014; Right) along Santa Catarina coast. Each oceanic pixel represents the spatial resolution data, 4 km^2, according to satellite Aqua, sensor MODIS. (Moderate Resolution Imaging Spectroradiometer).

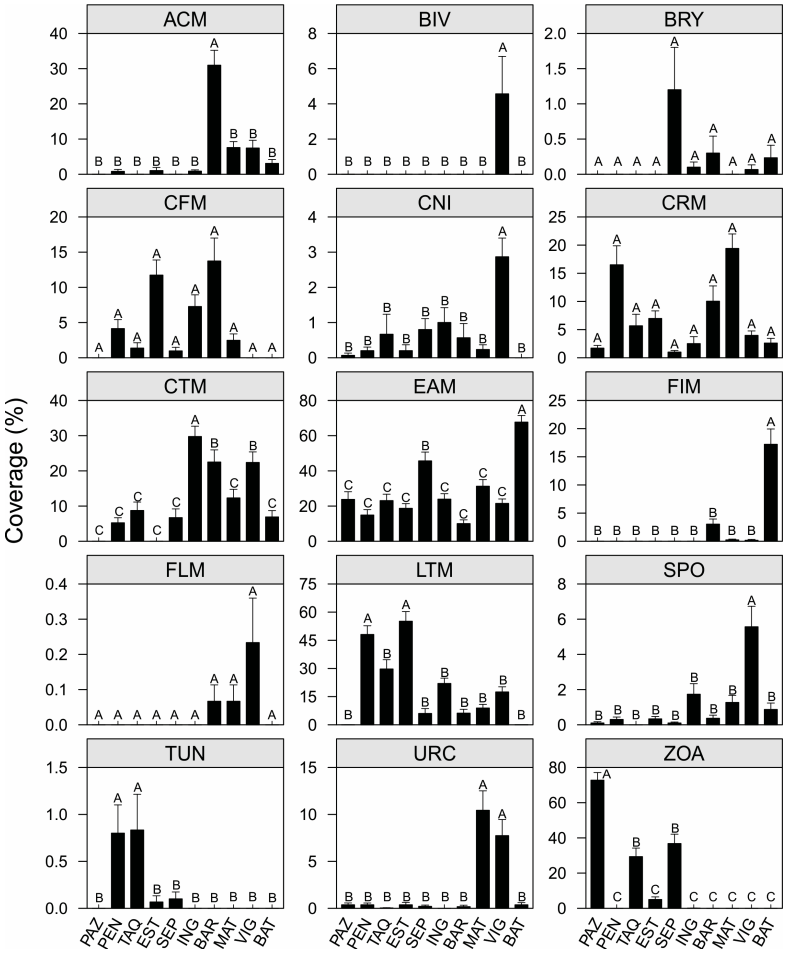


Figure 3 - Coverage percentage with error bars for group species in each site. Sites are ordered according to increasing latitudinal coordinates, which follow the decreasing SST gradient. Letters represent abundance differences among sites according to SNK test. PAZ = Paz Island, PEN = Penha, TAQ = Taquaras, EST = Estaleiro, SEP = Sepultura, ING = Ingleses, BAR = Barra da Lagoa, MAT = Matadeiro, VIG = Vigia, BAT = Batuta Island. ACM = Articulated calcareous macroalgae, BIV = Bivalve, BRY = Bryozoans, CFM = Corticated foliose macroalgae, CNI = Cnidarian, CRM = Crustose macroalgae, CTM = Corticated macroalgae, EAM = Ephilitic algal matrix, FIM = Filamentous algae,

FLM = Foliose macroalgae, LTM = Leathery macroalgae, SPO = Sponges, TUN = Tunicates, URC = Sea urchins, ZOA = Zoanthids.

3.2 Sites dissimilarity

The two axes of PCoA comprised 90.2% of total variation amongst sites (Figure 4). Every site was quite distinct from others. The PCoA2 axis show a distribution pattern, with two distinct groups formation. All locations further north (points red colored), that have subtropical characteristics, responded negatively to this axis, while central (green points) and southern sites (blue points) had a positive relationship with this axis.

Simper analysis indicate the group species responsible for the dissimilarities between sites: PAZ, the northernmost sampled site, has a community structure markedly different mainly by its high zoanthid (ZOA) abundances, that represent 72.77% (∓4.35) of total hard bottom coverage and was the assemblage responsible for the largest dissimilarity percentage to all other locations. SEP, the most similar site to PAZ, has 37% (∓5.33%) of ZOA abundance (ZOA was the dominant taxa in both), and this group accounts for 26% of total dissimilarity between these sites. Whilst, BAT, the southernmost site, also presented a very different community from other sites (Figure 4). This difference was primarily driven by EAM, which was also the most representative group in BAT, corresponding for almost 68% (∓3.79%) of benthic coverage. BAR and VIG, the most similar communities, show similar species composition and abundances. Usually the species that contributes the most for the differences among sites was the most abundant, and generally was dominant in one site and not in others.

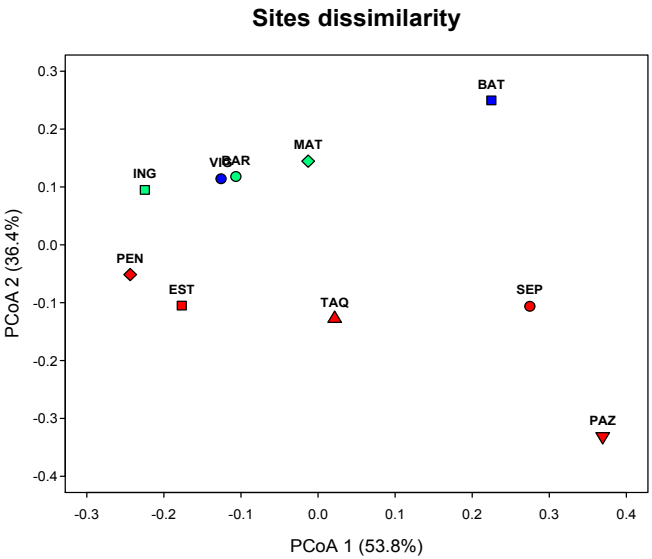


Figure 3 - Site dissimilarity PCoA biplot based on Bray-Curtis dissimilarity of the benthic community data. Each point is the centroid of the six transects sampled. PAZ = Paz Island, PEN = Penha, TAQ = Taquaras, EST = Estaleiro, SEP = Sepultura, ING = Ingleses, BAR = Barra da Lagoa, MAT = Matadeiro, VIG = Vigia, BAT = Batuta Island. ● = Barra da Lagoa, ■ = Ingleses, ◆ = Matadeiro, ● = Sepultura, ■ = Estaleiro, ◆ = Penha, ▲ = Taquaras, ▼ = Paz Island, ● = Vigia, ■ = Batuta Island

3.3 Hierarchical benthic community structure

The differences among hard bottom benthic community were mainly concentrated at the smallest spatial scale (i.e. replicated quadrats), which accounted for more than half of total variation observed (Table 1). Sites showed the second largest proportion of variation, and its importance was close to the quadrats. Transects do not show large variation.

3.4 Hierarchical distribution of functional/taxonomic groups

For the benthic functional/taxonomic groups, every group, including invertebrates and algae, nested-ANOVA results

indicate that the largest proportion of variance occur at the quadrat level, the smallest spatial scale incorporated into our study design (Table 2 and 3). The nested-ANOVA univariate data results indicated significant differences for benthic assemblages at every level. Filamentous algae (Table 2) and Zoanthids (Table 3), the only two excptions for the previous pattern, have the highest percentage of their variation concentrated in the higher sampling scale, sites (48.33% and 38.89%, respectively). Widely distributed assemblages (i. e. present in most of sites): Leathery macroalgaes (LTM), Corticated macroalgae (CTM) Crustose macroalgae (CRM) and Corticated macroalgae (CTM); or assemblages more equitatively distributed over the sites, as Cnidarians (CNI) and Ephilitic algal matrix (EAM), had all the quadrat level accounting for more than 50% of the total variation

Table 1 – PERMANOVA based on Bray-Curtis distances calculated on fourth root transformed relative abundances for sites, including estimates of variation at each spatial scale and its relative proportion.

	df	MS	Pseudo-*F*	*P* (perm)	Variation	Proportion
Site	9	71389	20.616	0.0001	1132.1	41.738
Transect	50	3462.7	2.526	0.0001	209.16	7.711
Quadrat	540	1371.1			1371.1	**50.55**
Total	599	71389			2712.4	100

Table 2 - Variance components (V.c.) and percentage variance components (%V.c.) for algae groups abundance among sites, transects and quadrats in Santa Catarina coast. Largest variance components are highlighted in bold. Differences among replications scales was significant at P<0.001 for every taxonomic/functional group.

	Leathery macroalgae		Corticated macroalgae		Foliose macroalgae		Corticated foliose macroalgae		Articulated calcareous macroalgae		Crustose macroalgae		Filamentous algae		Ephilitic algal matrix	
	V. c.	% V. c.	V. c.	% V. c.	V. c.	% V. c.	V. c.	% V. c.	V. c.	% V. c.	V. c.	% V. c.	V. c.	% V. c.	V. c.	% V. c.
Sites	0.295	37.425	0.031	35.615	0.002	8.701	0.090	26.896	0.150	34.041	0.104	26.301	0.102	**38.897**	0.229	32.938
Transects	0.158	20.088	0.003	10.967	0.006	22.155	0.064	19.105	0.115	26.115	0.071	18.113	0.004	23.912	0.080	11.452
Quadrat	0.335	**42.488**	0.070	**53.417**	0.018	**69.145**	0.180	**53.999**	0.176	**39.844**	0.219	**55.585**	0.009	37.190	0.386	**55.610**
Total	0.788	100	0.104	100	0.26	100	0.334	100	0.441	100	0.394	100	0.115	100	0.695	100

Table 3 - Variance components (V.c.) and percentage variance components (%V.c.) for invertebrates groups abundance among sites, transects and quadrats in Santa Catarina coast. Largest variance components are highlighted in bold**.** Differences among replications scales was significant at P<0.001 for every taxonomic/functional group.

	Sponges		Cnidarian		Zoanthids		Bryozoans		Sea urchin		Tunicates		Bivalve	
	V. c.	% V. c.	V. c.	% V. c.	V. c.	% V. c.	V. c.	% V. c.	V. c.	% V. c.	V. c.	% V. c.	V. c.	% V. c.
Sites	0.042	30.188	0.029	24.441	0.360	**48.335**	0.007	10.999	0.074	30.282	0.011	19.501	0.020	16.970
Transects	0.005	3.920	0.019	15.653	0.087	11.665	0.013	20.422	0.057	23.573	0.006	10.204	0.001	19.519
Quadrat	0.092	**65.892**	0.072	**59.907**	0.298	39.999	0.042	**68.579**	0.112	**46.145**	0.041	**70.295**	0.006	**63.511**
Total	0.139	100	0.120	100	0.745	100	0.62	100	0.243	100	0.58	100	0.27	100

3.5 Influence of abiotic variables over sessile benthic community structure

CAP analysis over 60 transects found a total of three constrained axis, which represent a total of 31.6% of total variation, and 24 unconstrained axis for residuals which are responsible for 68.4% of variation. For the multivariate variation explained, the first axis, CAP1 ($P = 0.001$) was responsible for 75% of the canonical variation and 23.7% for total variation and it was related to increasing temperature; while the second axis, CAP2 ($P = 0.002$) is responsible for 21.6% of total constrained variation and 7% for total variation being more related to low habitat complexity (Figure 5). The result indicate that the three abiotic variables analyzed significantly influence benthic community structure (Table 4).

Temperature drives the position of the northern sites, where almost every transect has a positive relation to CAP1, while the complexity of each transect is guiding CAP2. Paz Island (PAZ), Batuta Island (BAT) and Sepultura (SEP) are the most complex sites, whereas Penha (PEN) and Estaleiro (EST) are the least complex sites. Complexity seems to regulate leathery macroalgae (LTM) distribution, which are more abundant in low complexity transects, with a peak of distribution in low complexity sites (PEN and EST). Zoanthids (ZOA) have their distribution restricted to warm sites and their abundances are positively related to higher temperature means (Adjusted R-squared = 0.3749, $P<0.001$). Articulated calcareous macroalgae (ACM) and Corticated macroalgae (CTM) are more abundant in low temperature sites; Sponges (SPO) and Filamentous macroalgae (FIM) are more abundant in milder SST sites. Bottom slope is not associated with any assemblage distribution.

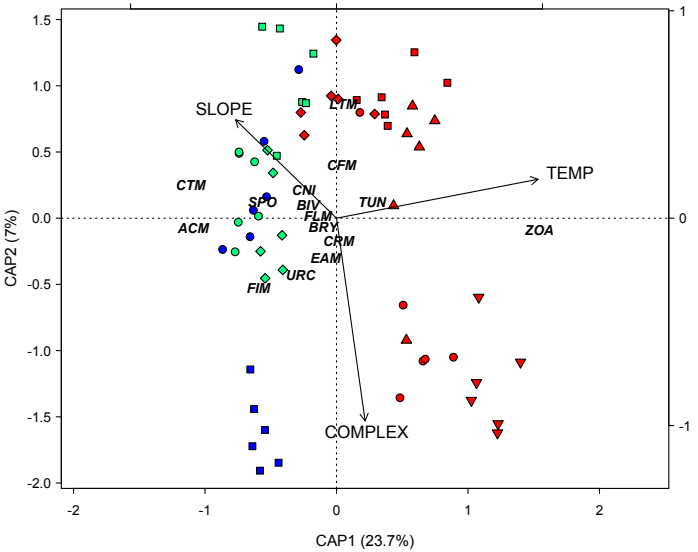


Figure 4 – Constrained Analisys of Principal Components (CAP) correlating abiotic variables to benthic species groups and sampling transects. COMPLEX = Substrate complexity, SLOPE = Bottom slope, TEMP = Mean Sea Superficial Temperature for Summer. LTM = Leathery macroalgae, CTM = Corticated macroalgae, FLM = Foliose macroalgae, CFM = Corticated foliose macroalgae, ACM = Articulated calcareous macroalgae, CRM = Crustose macroalgae, FIM = Filamentous algae, EAM = Ephilitic algal matrix, SPO = Sponges, CNI = Cnidarian, ZOA = Zoanthids, BRY = Bryozoans, URC = Sea urchins, TUN = Tunicates, BIV = Bivalve. ● = Barra da Lagoa, ■ = Ingleses, ◆ = Matadeiro, ● = Sepultura, ■ = Estaleiro, ◆ = Penha, ▲ = Taquaras, ▼ = Paz Island, ● = Vigia, ■ = Batuta Island

Table 4 - Analysis of variance for environmental variables over CAP

	df	SS	*F*	*P*
Complexity	1	0.5458	5.7073	0.001
Slope	1	0.4866	5.0880	0.001
Temperature	1	1.4393	15.0509	0.001
Residual	56	190.883		

4. Discussion

Along Santa Catarina coast there is a latitudinal pattern of species replacement following the decreasing temperature gradient, where zoanthids and leathery macroalgae are the dominant groups in places further north, with subtropical physiognomies while articulated calcareous, corticated and filamentous macroalgae have higher abundances in sites of temperate characteristics, further south. The highest variation was concentrated in the lower replicate scale for most of functional/taxonomic groups and for the entire benthic sessile community. Among the sampled abiotic variables, temperature was the most descriptive for community dissimilarities, followed by habitat complexity. Bottom slope has no great effect on benthic community structure.

4.1 Community structure

The total richness sampled (58 taxa) was lower than observed by another study conducted in Santa Catarina coastal islands in a smaller latitudinal range, which has found 111 taxa, 55 of these were new records for the study area (Bouzon et al. 2012). This difference of richness may be a result of sampling depth. While our study was focused in shallow waters (0-2 meters depth), Bouzon et al. (2012) sampled the benthic community in deeper substrates (6 m and 15 m) which can capture a wider range of diversity along the depth gradient with vertical replacement of species due to different hydrodynamics, exposure to waves and solar intensity (Oigman-Pszczol et al. 2004, Terlizzi et al. 2007, Valdivia et al. 2014).

Some assemblages are clearly distributed over sites following the latitudinal gradient, which represents a decrease in SST, occuring a species turnover pattern. The high abundance of zoanthids (ZOA) in northern sites is gradually replaced by fleshy algae, that have abundance increasing gradually southwards, as Articulated calcareous macroalgae (ACM); are restricted only in southern sites, as Filamentous macroalgae (FIM) or have relatively greater abundance in cold waters sites than in warm water northern sites, such as Corticated macroalgae (CTM). The distribution of Zoanthids, restricted to northern sites, may be due

to a sea surface temperature treshold, Reimer et al. 2008 has show for Pacific zoanthid species the temperature treshold of 16°C (were these cnidarians are unable to exist on sites with SST under 16°C). Previous studies conducted on Santa Catarina coast found the same distribution pattern of zoanthids, and in both the distribution limit was associated with low temperatures found in southern sites (Faria-Júnior 2014, Oliveira 2014), which may trigger a latitudinal replacement of zoanthids on warm water northern sites by fleshy algae on souther sites. Bryozoans (BRY) and Foliose macroalgae (FLM) are not much representative of benthic community, but like the previous assemblages, have a variation according to the latitudinal temperature gradient, indicating that temperature may also influence the allocation of low abundance species.

Some markedly higher abundance of functional/taxonomic groups in one of the sites may be a result of food chain disturbance/dynamics. For example, filamentous algae, which have a high abundance in only one site (BAT) may have their high abundances kept by low densities of its natural consumer, sea urchins, which presented low abundances in Batuta Island (BAT) and can directly feed on filamentous algae, exerting a strong top-down control (Bulleri et al., 1999; Guarnieri et al., 2014; Poore et al., 2012). In addition, the high complexity found in BAT may indirectly influence early successional algae abundances by keeping high diversity of browsing species responsible for feeding on climax algae. This peculiar distribution can also result from some different community dynamics discrepancy that interfere in species abundance or even a random effect since all groups have low abundances.

Some group species present an even distribution across sites (e. g. CFM, CNI, CRM and EAM), which may indicate that there is no outstanding feature on site scale that may influence their abundances. All these groups, except CNI, are more abundants related to other taxonomic/functional group, what may indicate that species with high abundance have greater stability to local variations or vaster range of use of resources.

4.2 Variation within hierarchical levels

Most variation observed in this study occurred at the smaller spatial scale, the quadrat level. This pattern was observed for most of taxonomic/functional groups as well for the entire benthic community structure. This result meets a recurring pattern for marine environments: that the largest variability is concentrated at the smallest sampled scale (Commito et al. 2006, Olabarria and Chapman 2006, Chapman et al. 2010, Sandrini-Neto and Lana 2011). This pattern probably is a result of patchy distribution, frequently demonstrated for almost all benthic populations and assemblages at varying habitats (rocky shores, unvegetated tidal flats and sublittoral soft-bottoms), suggesting that small-scale processes and interactions are very relevant in structuring marine benthic communities (Fraschetti et al. 2005). Therefore, despite the higher variance concentrated in our lower sampled level, quadrats, that among our sampled abiotic variables is more related to bottom slope, our results demonstrate no direct relation between slope and community structure. This may indicate the presence of different environmental variables regulating patchy distribution and creating a high variable horizontal distribution for benthic organisms. These divergences may be due to competition, grazing, availability of refugia (Díaz and McQuaid 2011, Valdivia et al. 2014), consumption, or simply the random settlement of benthic larvae.

The second most important scale explaining variances was sites, and large-scale abiotic variables might regulate their distributions. Filamentous algae (FIM) and Zoanthids (ZOA) were an exception for the emerging pattern, with the high variance occurring among sites (Table 2), and their distributions might be linked to a large-scale factor. The assemblage ZOA is composed by two zooxanthellate zoanthid species (*Palythoa caribaeorum* and *Palythoa grandiflora*), whose distributions are likely limited by an SST threshold around 16^{o}C (see Reimer et al., 2008 for Pacific species). In this study, the southern sites (with absence of zoanthids) have an 18^{o}C average SST during the winter, and the temperature probably extends under 16^{o}C, limiting the occurrence of zoanthids in these sites. Nevertheless, SST was not able to explain Filamentous macroalgae (FIM) distribution and its absence in northern sites. However, many different environmental factors covary with the latitudinal gradient, such as chlorophyll *a* and nutrient concentration, which

allow higher abundances in temperate regions, especially for algae, or environmental factors that can interfere in algal community composition in large scales, such as pollution, sediment loading, hydrodynamics, and habitat quality, which can explain filamentous algae distribution patterns (Díez et al., 2003; Tuya et al., 2012). Transects are particularly homogeneous and present the lowest variance for the community structure, indicating synchronous composition over transects inside sites.

4.3 Mechanisms controlling sessile benthic community structure

Our results indicate that among our sampled abiotic variables, temperature was the most important structuring process for the benthic community, and possibly responsible for restraining or decreasing many group species abundances. Several patterns emerge from this attribute, as the benthic structure pattern along the latitudinal increase. Leathery macroalgae (LTM) and Zoanthids (ZOA), which are dominant in northern sites and respectively more abundant in northern sites and absent in southern sites, have their coverage replaced southwards by Corticated macroalgae (CTM), Articulated calcareous macroalgae (ACM) and Filamentous macroalgae (FIM); these algal groups are negatively correlated to SST.

The absence os Zoanthids in temperate rocky shores (central and southern sites) probably allows a higher diversity of incrusting invertebrates as sponges, sea urchins and other cnidarian species, once zoanthids are great competitors for consolidated substrate and tend to exclude organisms that surround its limits (Suchaneck and Green 1981, Bastidas and Bone 1996, Mendonça-Neto and da Gama 2008). Fleshy algae usually have their abundance and richness increasing out of the tropics, in temperate regions, due to lower competition with cnidarians, which have distribution restriction in low SST habitats (Harriott and Banks 2002, Kerswell 2006, Reimer et al. 2008).

Although not strongly related to community change, habitat complexity was also very important for structuring some group species. Leathery macroalgae (LTM) show a tendency of distribution in low complexity transects, being absent in high

complexity sites (Figure 5). Over low complexity sites, distribution is not related to temperature and the low abundance of LTM in high complexity transects may be the result of a food chain disturbance leaded by this variable. High complexity environments house greater diversity of vertebrates; this provides higher abundances and diversity of browsing species (i. e. species that feed on leathery macroalgae, as *Sargassum* sp., playing an important role preventing late successional macroalgal-dominance) and may trigger food chain changes. The abundance of farmer fishes, as damselfish, may impact leathery macroalgae (LTM) abundance, delaying the successional process in rocky shores, maintaining a high abundance of filamentous algae instead of fleshy algae (Ceccarelli et al. 2011). Sea turtles are also active grazers of leathery macroalgae and can regulate their abundances (Goatley et al. 2012).

Based on previous studies, we hypothesized that bottom slope would have great importance in structuring benthic communities, especially for species that are better suited to habitats with high solar irradiation, such as photosynthetic organisms (Oigman-Pszczol et al. 2004), once high slope environments receive significantly lower levels of solar irradiance when compared to flat surfaces (Lesser et al. 2009). Likewise, different inclinations may influence growth and survival rates due to different levels along the slope sedimentation gradient (Babcock and Mundy 1996). Nevertheless, our hypothesis was refuted. Slope was the least important abiotic variable in explaining community variation and was not related to any group species distribution, not playing a key role as a structuring process of the shallow benthic community in micro-scale.

However, the deterministic relationship between inclination and solar radiation has been well established in the literature but more evident in mesophotic regions where irradiance is limited by depth (Bridge et al. 2011). A possible explanation for our result is that, in very shallow waters, solar radiation is able to dissipate more equally in different substrate slopes. Oigman-Pszczol et al. (2004) have found a shift species pattern over steeper and smooth rocky shore slope in tropical Brazilian shallow waters, but their method to evaluate inclination

was not effective in measuring differences in micro scale, since the measures were made within a transect (10s of meters). Frequently, in rocky shores, differences in slope occur in lower scale (10s of centimeters), covering slope patchy distribution patterns.

5. Conclusions

Our results suggest that along Santa Catarina coast there is a species shift pattern over the latitudinal gradient of zoanthids and leathery macroalgae, more abundant in northern subtropical sites, being replaced by articulated calcareous, corticated and filamentous macroalgae in southern temperate sites.

The distribution of shallow-water marine benthic community in Santa Catarina follows a recurring pattern for marine organisms: that the greater variability among samples is concentrated in the lower sampling level, possibly due to the patchy distribution of organisms and other micro-processes.

Among the sampled process, temperature was the abiotic variable that best explained the community variations, regulating zoanthids distribution over sites. Habitat complexity was the second most important process on regulating benthic structure influencing leathery macroalgae distribution over low complexity sites.

Bottom slope was hypothesized to have a high influence on benthic community distribution, but our results show no direct relation, possibly due to the shallow depth extract where this study was performed, which allows the solar radiation to dissipate equaly over different inclination levels.

Thus, other studies trying to identify what micro-scale processes drive dissimilarities between sites are suggested to to further address this question.

References:

Acha, E. M., H. W. Mianzan, R. A. Guerrero, M. Favero, and J. Bava. 2004. Marine fronts at the continental shelves of austral South America. Journal of Marine Systems 44:83–105.

Aguilera, M. A., B. R. Broitman, and M. Thiel. 2014. Spatial variability in community composition on a granite breakwater versus natural rocky shores: lack of microhabitats suppresses intertidal biodiversity. Marine pollution bulletin 87:257–68.

Airoldi, L. 2003. The effects of sedimentation on rocky coast assemblages. Oceanography and Marine Biology 41:161–236.

Anderson, A. B., A. Carvalho-filho, R. A. Morais, L. T. Nunes, J. P. Quimbayo, and S. R. Floeter. 2015. Brazilian tropical fishes in their southern limit of distribution: checklist of Santa Catarina's rocky reef ichthyofauna, remarks and new records 11.

Anderson, M. J. 2001. A new method for non parametric multivariate analysis of variance. Austral ecology 26:32–46.

Anderson, M. J., R. N. Gorley, and K. R. Clarke. 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods.

Anderson, M. J., and J. Robinson. 2003. Generalised discriminant analysis based on distances. Australian and New Zealand Journal of Statistics 45:301–318.

Anderson, M. J., and D. C. I. Walsh. 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? Ecological Monographs 83:557–574.

Anderson, M. J., and T. J. Willis. 2003. Canonical Analysis of Principle Coordinates: AA useful method of constrined ordination for ecology. Ecology 84:511–525.

Babcock, R., and C. Mundy. 1996. Coral recruitment: Consequences of settlement choice for early growth and survivorship in two scleractinians. Journal of Experimental Marine Biology and Ecology 206:179–201.

Bastidas, C., and D. Bone. 1996. Competitive strategies between Palythoa caribaeorum and Zoanthus sociatus (Cnidaria: Anthozoa) at a reef flat environment in Venezuela. Bulletin of Marine Science 59:543–555.

Bellwood, D. R. 2003. Origins and escalation of herbivory in fishes: a functional perspective. Paleobiology 29:71–83.

Benedetti-Cecchi, L. 2001. Variability in abundance of algae and invertebrates at different spatial scales on rocky sea shores. Marine Ecology Progress Series 215:79–92.

Bloch, C. P., and B. T. Klingbeil. 2015. Anthropogenic factors and habitat complexity influence biodiversity but wave exposure drives species turnover of a subtropical rocky inter-tidal

metacommunity. Marine Ecology 1:1–13.

Borcard, D., F. Gillet, and P. Legendre. 2011. Numerical Ecology with R.

Bouzon, J., F. P. Brandini, and R. M. Rocha. 2012a. Biodiversity of Sessile Fauna on Rocky Shores of Coastal Islands in Santa Catarina, Southern Brazil. Marine Science 2:39–47.

Bouzon, J., F. P. Brandini, and R. M. Rocha. 2012b. Biodiversity of Sessile Fauna on Rocky Shores of Coastal Islands in Santa Catarina, Southern Brazil. Marine Science 2:39–47.

Bridge, T. C. L., T. J. Done, R. J. Beaman, a. Friedman, S. B. Williams, O. Pizarro, and J. M. Webster. 2011. Topography, substratum and benthic macrofaunal relationships on a tropical mesophotic shelf margin, central Great Barrier Reef, Australia. Coral Reefs 30:143–153.

Bulleri, F., L. Benedetti-Cecchi, and F. Cinelli. 1999. Grazing by the sea urchins Arbacia lixula L. and Paracentrotus lividus Lam. in the Northwest Mediterranean. Journal of Experimental Marine Biology and Ecology 241:81–95.

Capel, K. C. C., B. Segal, P. Bertuol, and A. Lindner. 2012. Corallith beds at the edge of the tropical South Atlantic. Coral Reefs.

Castro, C. B., and D. O. Pires. 2001. Brazilian Coral Reefs: What we alredy know and what is still missing. Bulletin of Marine Science 69:357–371.

Ceccarelli, D. M., G. P. Jones, and L. J. McCook. 2011. Interactions between herbivorous fish guilds and their influence on algal succession on a coastal coral reef. Journal of Experimental Marine Biology and Ecology 399:60–67.

Chapman, M. G. 2002. Patterns of spatial and temporal variation of macrofauna under boulders in a sheltered boulder field. Austral Ecology 27:211–228.

Chapman, M., T. Tolhurst, R. Murphy, and A. Underwood. 2010. Complex and inconsistent patterns of variation in benthos, micro-algae and sediment over multiple spatial scales. Marine Ecology Progress Series 398:33–47.

Coleman, M. . 2002. Small-scale spatial variability in intertidal and subtidal turfing algal assemblages and the temporal generality of these patterns. Journal of Experimental Marine Biology and Ecology 267:53–74.

Commito, J. a., W. E. Dow, and B. M. Grupe. 2006. Hierarchical spatial structure in soft-bottom mussel beds. Journal of Experimental Marine Biology and Ecology 330:27–37.

Connell, S. D. 2005. Assembly and maintenance of subtidal habitat heterogeneity : synergistic effects of light penetration and sedimentation. Marine Ecology Progress Series 289:53–61.

Creed, J. C. 2006. Two invasive alien azooxanthellate corals, Tubastraea

coccinea and Tubastraea tagusensis, dominate the native zooxanthellate Mussismilia hispida in Brazil. Coral Reefs.

Díaz, E. R., and C. D. McQuaid. 2011. A spatially explicit approach to trophic interactions and landscape formation: patchiness in small-scale variability of grazing effects along an intertidal stress gradient. Journal of Ecology 99:416–430.

Díez, I., A. Santolaria, and J. . Gorostiaga. 2003. The relationship of environmental factors to the structure and distribution of subtidal seaweed vegetation of the western Basque coast (N Spain). Estuarine, Coastal and Shelf Science 56:1041–1054.

Drummond, S. P., and S. D. Connell. 2005. Quantifying percentage cover of subtidal organisms on rocky coasts: A comparison of the costs and benefits of standard methods. Marine and Freshwater Research 56:865–876.

Eidens, C., T. Hauffe, E. Bayraktarov, C. Wild, and T. Wilke. 2015. Multi-scale processes drive benthic community structure in upwelling-affected coral reefs. Frontiers in Marine Science 2:1–11.

Fabricius, K. E. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Marine pollution bulletin 50:125–46.

Faria-Júnior, E. 2014. Distribuição espacial e estrutura das comunidades de antozoários (cnidaria: anthozoa) em substratos consolidados no litoral de santa catarina, sul do Brasil. Dissertação (mestrado) Programa de Pós-Graduação em Ecologia - Universidade Federal de Santa Catarina.

Fernandez, M. O., S. A. Navarrete, and A. C. Marques. 2015. A comparison of temporal turnover of species from benthic cnidarian assemblages in tropical and subtropical harbours. Marine Biology Research 11:492–503.

Fitt, W., B. Brown, M. Warner, and R. Dunne. 2001. Coral bleaching: interpretation of thermal tolerance limits and thermal thresholds in tropical corals. Coral Reefs 20:51–65.

Floeter, S. R., M. D. Behrens, C. E. L. Ferreira, M. J. Paddack, and M. H. Horn. 2005. Geographical gradients of marine herbivorous fishes: Patterns and processes. Marine Biology 147:1435–1447.

Floeter, S. R., L. A. Rocha, D. R. Robertson, and J. C. Joyeux. 2008a. Atlantic reef fish biogeography and evolution. Journal of Biogeography:22–47.

Floeter, S. R., L. A. Rocha, D. R. Robertson, J. C. Joyeux, W. F. Smith-Vaniz, P. Wirtz, A. J. Edwards, J. P. Barreiros, C. E. L. Ferreira, J. L. Gasparini, A. Brito, J. M. Falc??n, B. W. Bowen, and G. Bernardi. 2008b. Atlantic reef fish biogeography and evolution. Journal of Biogeography 35:22–47.

Flores, A. A. V., R. A. Christofoletti, A. L. F. Peres, A. M. Ciotti, and S.

A. Navarrete. 2015. Interactive effects of grazing and environmental stress on macroalgal biomass in subtropical rocky shores: Modulation of bottom-up inputs by wave action. Journal of Experimental Marine Biology and Ecology 463:39–48.

Fraschetti, S., C. N. Bianchi, A. Terlizzi, G. Fanelli, C. Morri, and F. Boero. 2001. Spatial variability and human disturbance in shallow subtidal hard bottom assemblages: a regional approach. Marine Ecology Progress Series 212:1–12.

Fraschetti, S., A. Terlizzi, and L. Benedetti-cecchi. 2005. Patterns of distribution of marine assemblages from rocky shores : Evidence of relevant scales of variation. Marine Ecology Progress Series 296:13–29.

Garrabou, J., E. Ballesteros, and M. Zabala. 2002. Structure and Dynamics of North-western Mediterranean Rocky Benthic Communities along a Depth Gradient. Estuarine, Coastal and Shelf Science 55:493–508.

Goatley, C. H. R., A. S. Hoey, and D. R. Bellwood. 2012. The Role of Turtles as Coral Reef Macroherbivores. PLoS ONE 7:e39979.

Grigg, R. W. 1995. Coral reefs in an urban embayment in Hawaii: a complex case history controlled by natural and anthropogenic stress. Coral Reefs 14:253–266.

Guarnieri, G., S. Bevilacqua, F. Vignes, and S. Fraschetti. 2014. Grazer removal and nutrient enrichment as recovery enhancers for overexploited rocky subtidal habitats. Oecologia 175:959–970.

Harriott, V., and S. Banks. 2002. Latitudinal variation in coral communities in eastern Australia: a qualitative biophysical model of factors regulating coral reefs. Coral Reefs 21:83–94.

Jackson, J. B. 2001. What was natural in the coastal oceans? Proceedings of the National Academy of Sciences of the United States of America 98:5411–5418.

Johnson, M. P., R. N. Hughes, M. T. Burrows, and S. J. Hawkins. 1998. Beyond the predation halo: small scale gradients in barnacle populations affected by the relative refuge value of crevices. Journal of Experimental Marine Biology and Ecology 231:163–170.

Jokiel, P. L. 1980. Solar ultraviolet radiation and coral reef epifauna. Science 207:1069–1071.

Kerswell, A. P. 2006. Global biodiversity patterns of benthic marine algae. Ecology 87:2479–2488.

Kramer, M. J., D. R. Bellwood, and O. Bellwood. 2012. Cryptofauna of the epilithic algal matrix on an inshore coral reef, Great Barrier Reef. Coral Reefs 31:1007–1015.

Lages, B. G., B. G. Fleury, C. Menegola, and J. C. Creed. 2011. Change in tropical rocky shore communities due to an alien coral invasion. Marine Ecology Progress Series 438:85–96.

Lesser, M. P., M. Slattery, and J. J. Leichter. 2009. Ecology of mesophotic coral reefs. Journal of Experimental Marine Biology and Ecology 375:1–8.

Llabrés, M., S. Agustí, M. Fernández, A. Canepa, F. Maurin, F. Vidal, and C. M. Duarte. 2013. Impact of elevated UVB radiation on marine biota: a meta-analysis. Global Ecology and Biogeography 22:131–144.

Madin, J. S., and S. R. Connolly. 2006. Ecological consequences of major hydrodynamic disturbances on coral reefs. Nature 444:477–480.

McArdle, B. H., and M. J. Anderson. 2001. Fitting multivariate models to community data: A comment on distance-based redundancy analysis. Ecological Society of America 82:290–297.

McCook, L. J. 1999. Macroalgae, nutrients and phase shifts on coral reefs: Scientific issues and management consequences for the Great Barrier Reef. Coral Reefs 18:357–367.

McCook, L. J., J. Jompa, and G. Diaz-Pulido. 2001. Competition between corals and algae on coral reefs: A review of evidence and mechanisms. Coral Reefs 19:400–417.

Mendonça-Neto, J. P., and B. a. P. da Gama. 2008. The native Palythoa caribaeorum overgrows on invasive species in the intertidal zone. Coral Reefs 28:497–497.

Menge, B. A., B. A. Daley, P. A. Wheeler, E. Dahlhoff, E. Sanford, and P. T. Strub. 1997. Benthic-pelagic links and rocky intertidal communities: Bottom-up effects on top-down control? Proceedings of the National Academy of Sciences 94:14530–14535.

Miller, M. W., and M. E. Hay. 1996. Coral-Seaweed-Grazer-Nutrient Temperate Reefs1. Ecological Monographs 66:323–344.

Mizrahi, D., S. A. Navarrete, and A. A. V. Flores. 2014. Uneven abundance of the invasive sun coral over habitat patches of different orientation: An outcome of larval or later benthic processes? Journal of Experimental Marine Biology and Ecology 452:22–30.

Oigman-Pszczol, S. S., M. A. de O. Figueiredo, and J. C. Creed. 2004. Distribution of Benthic Communities on the Tropical Rocky Subtidal of Armacao dos Buzios, Southeastern Brazil. Marine Ecology 25:173–190.

Oksanen, J., F. Blanchet, R. Kindt, P. Legendre, and R. O'Hara. 2016. Vegan: community ecology package. R package 2.3-3:Available at: https://cran.r–project.org/web/packa.

Olabarria, C., and M. G. Chapman. 2006. Comparison of patterns of spatial variation of microgastropods between two contrasting intertidal habitats. Marine Ecology Progress Series 220:201–211.

Piola, A. R., E. J. D. Campos, O. O. Möller Jr., M. Charo, and C.

Martinez. 2000. Subtropical Shelf Front off eastern South America. Journal of Geophysical Research 105:6565–6578.

Polunin, N. V. C., and M. Roberts. 1993. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. Marine Ecology Progress Series 100:167–176.

Poore, A. G. B., A. H. Campbell, R. A. Coleman, G. J. Edgar, V. Jormalainen, P. L. Reynolds, E. E. Sotka, J. J. Stachowicz, R. B. Taylor, M. A. Vanderklift, and J. Emmett Duffy. 2012. Global patterns in the impact of marine herbivores on benthic primary producers. Ecology Letters 15:912–922.

Prather, B. E., C. O'Byrne, C. Pirmez, and Z. Sylvester. 2016. Sediment Partitioning, Continental Slopes and Base-of-slope Systems. Basin Research:n/a–n/a.

Puente, A., and R. J. Diaz. 2015. Response of benthos to ocean outfall discharges: does a general pattern exist? Marine pollution bulletin 101:174–181.

R Development Core Team. 2013. R Development Core Team.

Reimer, J. D., S. Ono, F. Sinniger, and J. Tsukahara. 2008. Distribution of zooxanthellate zoanthid species (Zoantharia: ANthozoa: Hexacorallia) in southern Japan limited by cold temperatures. Galaxea, Journal of Coral Reef Studies 10:57–67.

Sandrini-Neto, L., and M. G. Camargo. 2012. GAD: an R package for ANOVA designs from general principles.

Sandrini-Neto, L., and P. C. Lana. 2011. Distribution patterns of the crab Ucides cordatus (Brachyura, Ucididae) at different spatial scales in subtropical mangroves of Paranaguá Bay (southern Brazil). Helgoland Marine Research 66:167–174.

Sarkar, D. 2008. Lattice: multivariate data visualization with R. (Springer, Ed.). New York.

Smith, J. E., C. M. Smith, and C. L. Hunter. 2001. An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. Coral Reefs 19:332–342.

Steneck, R. S., and M. N. Dethier. 1994. A functional group approach to the structure of algal-dominated communities. Oikos 69:476–498.

Suchaneck, T. H., and D. J. Green. 1981. Interspecific competition between Palythoa caribaeorum and other sessile invertebrates on St. Croix, US Virgin Islands. Proceedings of the Fourth International Coral Reef Symposium, Manila 1981:679–684.

Terlizzi, A., M. J. Anderson, S. Fraschetti, and L. Benedetti-Cecchi. 2007. Scales of spatial variation in Mediterranean subtidal sessile assemblages at different depths. Marine Ecology Progress Series 332:25–39.

Trygonis, V., and M. Sini. 2012. photoQuad: A dedicated seabed image processing software, and a comparative error analysis of four

photoquadrat methods. Journal of Experimental Marine Biology and Ecology 424-425:99–108.

Tuya, F., E. Cacabelos, P. Duarte, D. Jacinto, J. Castro, T. Silva, I. Bertocci, J. Franco, F. Arenas, J. Coca, and T. Wernberg. 2012. Patterns of landscape and assemblage structure along a latitudinal gradient in ocean climate. Marine Ecology Progress Series 466:9–19.

Underwood, A. ., M. . Chapman, and S. . Connell. 2000. Observations in ecology: you can't make progress on processes without understanding the patterns. Journal of Experimental Marine Biology and Ecology 250:97–115.

Underwood, A. J. 1997. Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance. Cambridge University Press, Cambridge.

Valdivia, N., M. J. Díaz, J. Holtheuer, I. Garrido, P. Huovinen, and I. Gómez. 2014. Up, down, and all around: scale-dependent spatial variation in rocky-shore communities of Fildes Peninsula, King George Island, Antarctica. PloS one 9:e100714.

WCS-Fiji. 2010. WCS-Fiji Marine Biological Monitoring Handbook Version 3:34.

Williams, G. J., J. E. Smith, E. J. Conklin, J. M. Gove, E. Sala, and S. A. Sandin. 2013. Benthic communities at two remote Pacific coral reefs: effects of reef habitat, depth, and wave energy gradients on spatial patterns. PeerJ 1:e81.

Wilson, S., and D. R. Bellwood. 1997. Cryptic dietary components of territorial damselfishes (Pomacentridae, Labroidei). Marine Ecology Progress Series 153:299–310.

Wilson, S. K., N. a. J. Graham, and N. V. C. Polunin. 2007. Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. Marine Biology 151:1069–1076.

Witman, J. D., R. J. Etter, and F. Smith. 2004. The relationship between regional and local species diversity in marine benthic communities : A global perspective. Proceedings of the National Academy of Sciences of the United States of America 101:15664–9.

Witman, J. D., R. W. Lamb, and J. E. K. Byrnes. 2015. Towards an integration of scale and complexity in marine Ecology. Ecological Monographs 85:475–504.

SUPLEMENTARY MATERIAL

Supplementary Table 1 – List of sampled species distributed over its functional/taxonomic groups along ten sampled sites. Sites are ordered according to increasing latitudinal coordinates. PAZ = Paz Island, PEN = Penha, TAQ = Taquaras, EST = Estaleiro, SEP = Sepultura, ING = Ingleses, BAR = Barra da Lagoa, MAT = Matadeiro, VIG = Vigia, BAT = Batuta Island.

Group / *Taxa*	PAZ	PEN	TAQ	EST	SEP	ING	BAR	MAT	VIG	BAT
Leathery macroalgae										
Palisada fragellifera					*x*		*x*			
Sargassum sp.	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	
Corticated macroalgae										
Acantophora spicifera			*x*		*x*					
Asparagopsis taxiformis						*x*				
Codium decorticatum					*x*	*x*	*x*	*x*	*x*	
Codium isthmocladum						*x*		*x*		
Gracilaria sp.						*x*				
Hypnea musciformis		*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	
Pterocladiella capilácea					*x*	*x*	*x*	*x*	*x*	*x*
Foliose macroalgae										
Ulva fasciata							*x*	*x*	*x*	
Corticated foliose macroalgae										
Dictyota spp.		*x*	*x*	*x*		*x*	*x*	*x*		
Lobophora variegata			*x*	*x*						
Padyna gimnospora		*x*	*x*	*x*	*x*	*x*				
Spatoglossum variabile		*x*								
Articulated calcareous macroalgae										
Amphiroa sp.				*x*		*x*	*x*			*x*
Arthrocardia flabellata						*x*	*x*	*x*	*x*	*x*
Dichotomaria marginata		*x*		*x*						
Jania sp.						*x*	*x*	*x*		*x*
Crustose macroalgae										
Codium intertextum		*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*
Colpomenia sinuosa		*x*		*x*	*x*	*x*	*x*	*x*	*x*	
Incrustose calcareous algae	*x*	*x*	*x*	*x*	*x*		*x*	*x*	*x*	*x*
Filamentous algae										
Aglaothamnion sp.							*x*	*x*	*x*	*x*
Cladophoropsis sp.										*x*
Spyridia sp.										*x*
Ephilitic algal matrix										
Ephilitic algal matrix	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*
Sponges										
Callyspongia pseudotoxa								*x*		
Clathria(Thalysias) sp.									*x*	
Dragmacidon reticulatum									*x*	
Dragmaxia anômala		*x*							*x*	
Haliclona vansoestti								*x*		
Hemimycale sp.		*x*								*x*
Hymeniacidon heliophila									*x*	
Mycale (Carmia) *microsigmatosa*		*x*		*x*	*x*	*x*	*x*	*x*		
Mycale angulosa				*x*						
Polymastia janeirensis									*x*	
Scopalina ruetzleri	*x*									
Suberites aurantiacus						*x*			*x*	*x*
Tedania ignis	*x*	*x*		*x*		*x*	*x*	*x*	*x*	*x*
Cnidarian										
Anemonia sargassensis							*x*			
Bunodosoma caissarum	*x*	*x*	*x*		*x*		*x*	*x*	*x*	*x*
Epiphityc Hydrozoan			*x*	*x*					*X*	
Sertularia marginata		*x*		*x*		*x*	*x*		*x*	
Zoanthids										
Macrocnemina sp.						*x*				

Palythoa caribaeorum	*x*		*x*	*x*	*x*						
Palythoa variabilis				*x*							
Bryozoans											
Bryozoa sp.					*x*					*x*	
Schizoporella errata						*x*	*x*				*x*
Sea urchins											
Arbacia lixula				*x*						*x*	*x*
Echinometra lucunter	*x*	*x*	*x*	*x*	*x*		*x*	*x*	*x*	*x*	*x*
Paracentrotus gaimardi								*x*	*x*	*x*	*x*
Tunicates											
Botrylloides nigrum		*x*			*x*						
Didemnum perlucidum		*x*	*x*								
Didemnum psammathodes			*x*								
Lissoclinum fragile		*x*	*x*	*x*							
Polysyncraton amethysteum		*x*	*x*	*x*							
Trididemnum sp.		*x*									
Bivalve											
Brachidontes solisianus										*x*	
Perna perna										*x*	

Supplementary Table 2 – Table of levels of substrate complexity for visual estimation.

Complexity level	Feautures
0	No vertical relief, large rocks with no burrows formation
1	Low and sparse relief
2	Low but widespread relief
3	Moderately complex, forming small burrows
4	Very complex with numerous burrows and fissures
5	Exceptionally complex with predominat vertical relief, and numerous caves and overhangs

Supplementary Table 3 – Mean Superficial Sea Temperature (SST) according to satellite Aqua, sensor MODIS (Moderate Resolution Imaging Spectroradiometer) over a spatial resolution of 4 km^2 for the summer of the last ten years (December up to March). $\mu 1$ = overall mean SST for the same site over the last ten years. $\mu 2$ = overall mean SST for the summer period over Santa Catarina state for ten sites. σ = standard deviation**.** PAZ = Paz Island, PEN = Penha, TAQ = Taquaras, EST = Estaleiro, SEP = Sepultura, ING = Ingleses, BAR = Barra da Lagoa, MAT = Matadeiro, VIG = Vigia, BAT = Batuta Island.

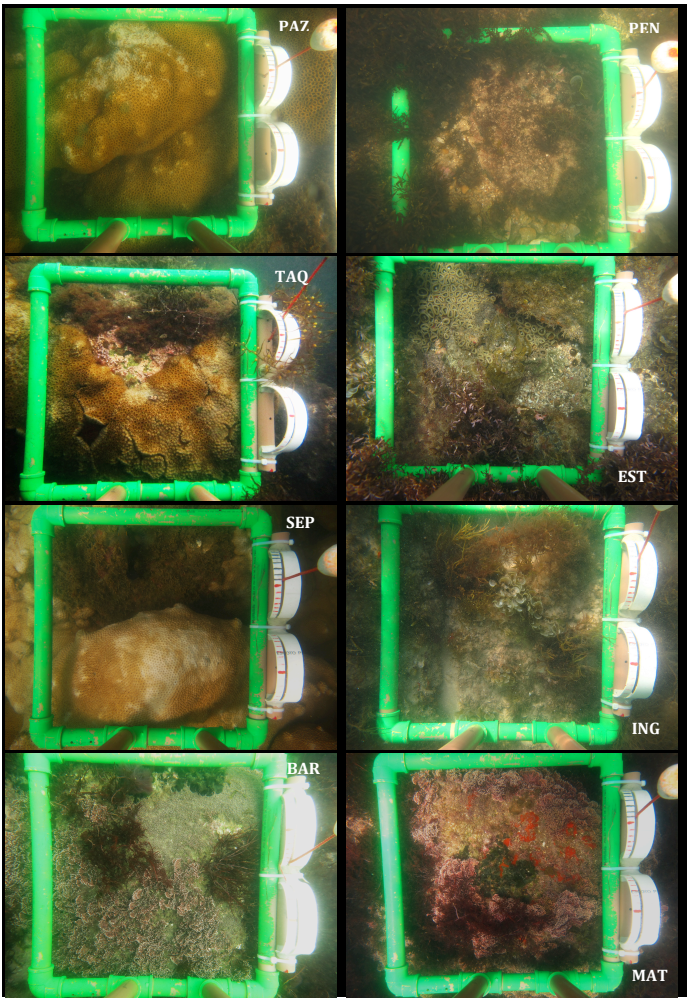
Local	2015	2014	2013	2012	2011	2010	2009	2008	2007	2006	μ_1
PAZ	26.31	26.79	25.69	25.72	25.50	26.58	26.00	26.21	26.42	26.34	**26.16**
PEN	26.07	25.46	25.55	26.48	25.46	25.40	26.06	25.21	26.13	26.00	**25.78**
TAQ	25.85	25.83	24.81	25.46	25.63	25.79	25.38	25.56	25.96	26.00	**25.63**
EST	25.78	25.58	24.92	25.42	25.70	26.20	25.85	25.27	25.83	26.15	**25.67**
SEP	25.56	25.37	24.71	25.07	25.27	26.22	25.29	25.29	25.82	25.77	**25.44**
ING	2435	24.12	24.11	23.22	24.01	24.74	24.23	23.89	24.43	25.34	**24.24**

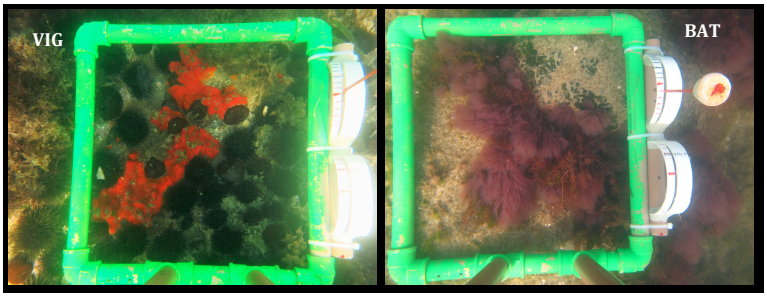
BAR	24.39	23.78	24.01	23.11	24.09	23.87	23.79	23.96	23.89	25.04	**23.99**
MAT	24.12	23.53	23.95	22.02	23.90	24.88	23.48	23.48	23.46	24.57	**23.74**
VIG	23.29	23.49	23.19	22.38	23.28	24.36	22.55	22.90	23.26	24.39	**23.31**
BAT	23.21	23.98	23.28	22.36	23.84	24.07	22.35	22.80	22.92	24.42	**23.32**
μ_2	24.89	24.79	24.42	24.12	24.67	25.21	24.50	24.45	24.81	25.40	**24.73**
σ	1.159	1.150	0.860	1.663	0.923	0.967	1.413	1.198	1.355	0.754	**1.110**

Supplementary Table 3 – Table of sites feautures, including geographical position, date of sampling and the orientation of the rochy sampled. PAZ = Paz Island, PEN = Penha, TAQ = Taquaras, EST = Estaleiro, SEP = Sepultura, ING = Ingleses, BAR = Barra da Lagoa, MAT = Matadeiro, VIG = Vigia, BAT = Batuta Island.

Site	Latitude	Longitude	Date	Orientation of the rocky shore
PAZ	26°17’	48°48’	02/02/15	West
PEN	26°77’	48°60’	01/31/15	North
TAQ	27°01’	48°57’	01/30/15	North
EST	27°12’	48°51’	01/22/15	Norteast
SEP	27°14’	48°47’	01/22/15	West
ING	27°44’	48°36’	01/13/15	Northwest
BAR	27°57’	48°41’	01/14/15	North
MAT	27°75’	48°49’	01/26/15	Northwest
VIG	28°01’	48°61’	03/08/15	Northwest
BAT	28°15’	48°64’	12/04/15	West

Supplementary Figure 1 – One representative quadrat for each ten sampled sites. PAZ = Paz Island, PEN = Penha, TAQ = Taquaras, EST = Estaleiro, SEP = Sepultura, ING = Ingleses, BAR = Barra da Lagoa, MAT = Matadeiro, VIG = Vigia, BAT = Batuta Island.




VIG
BAT